# CUMULATIVE MORTALITY AND POPULATION PARAMETERS FOR A VULNERABLE SEABIRD, THE RAZORBILL, ALCA TORDA, IN ATLANTIC CANADA

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# CUMULATIVE MORTALITY AND POPULATION PARAMETERS FOR A VULNERABLE SEABIRD, THE RAZORBILL *ALCA TORDA*, IN ATLANTIC CANADA

By

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## ABSTRACT

This thesis was developed within the framework of a conservation project to examine the demographics of a long-lived seabird, the Razorbill *Alca torda*, across its North American breeding range. Research was designed to (a) take advantage of two relatively long-term Razorbill capture-mark-recapture and productivity data sets available for two representative breeding islands in different oceanic regimes and (b) fill in research gaps to predict Razorbill population trends under various scenarios. I quantified the impacts of intraspecific kleptoparasitism, dispersal, fox predation, and hunting bycatch on the population parameters of the Razorbill at the Gannet Islands, Labrador and Machias Seal Island, New Brunswick. The level of intraspecific kleptoparasitism on the Gannet Islands is the highest reported for any seabird species (attack rate = 0.69, success rate = 0.18-0.22) and is implicated in the low productivity rates observed. Productivity at the Gannet Islands during 2004-2006 was the lowest reported since monitoring began in the 1980s, with only 39% of pairs successfully producing a chick. Long-distance breeding dispersal was more frequent than previously thought; distances moved by 40 birds ranged from 60 km to more 3,210 km. My estimates of adult and pre-breeder survival during 1995-2006 (Gannet Islands: 0.890 and 0.482 respectively; Machias Seal Island: 0.967 and 0.778 respectively) contrasted sharply with other studies. Specifically, adult survival at the Gannet Islands was the lowest ever reported for the species, and at Machias Seal Island it was the highest ever reported. The projected growth rate ($\lambda$) for the Gannet Islands Razorbill population predicted by models was 0.9475 for the Gannet Islands and 1.0613 for Machias Seal Island. Modeling also suggested that hunting mortality reduced the Gannet Islands projected population growth rate by 0.0603, while fox predation reduced population growth by 0.0126.

Together these sources reduced the projected population growth rate by 0.0729. Although the Razorbill population on Machias Seal Island appears to be growing, without substantial immigration the Gannet Islands population is expected to decline. The Gannet Islands Razorbill population is the largest in North America and therefore represents a significant conservation concern. Recommendations for the continued monitoring of both populations and development of specific management plans to control foxes on the Gannet Islands and investigate hunting bycatch are discussed.

CO-AUTHORSHIP STATEMENT

Chapters 2 through 6 are co-authored by my advisor Ian L. Jones. Dr. Jones provided both personal and research related financial support, shared in the design of the project, directed capture-mark-recapture data collection at the Gannet Islands starting in 1996, and contributed to the presentation of the results. Antony W. Diamond (University of New Brunswick) is a co-author on Chapters 3, 4, and 6. Dr. Diamond contributed to conceptual development of these chapters and provided funding to support the collection of 12 years of capture-mark-recapture data for Machias Seal Island, NB which was utilized in this thesis. Chapters 4 and 6 are co-authored by Gregory J. Robertson (Environment Canada) who assisted in the development of the population model presented in Chapter 6, and assisted with modeling survival rates in Chapter 4.

Publications (published or anticipated) and authorship arising from this thesis are:

Chapter 2 Lavers, J. L. and Jones, I. L. Effects of band resighting error on survival estimates in Razorbills (*Alca torda*) with implications for other bird studies.

Chapter 3 Lavers, J. L., Jones, I. L., and Diamond, A. W. Natal and breeding dispersal of Razorbills (*Alca torda*) in Atlantic Canada.

Chapter 4 Lavers, J. L., Jones, I. L., Diamond, A. W., and Robertson, G. J. Annual survival of Atlantic Canadian Razorbills (*Alca torda*) varies with climate and oceanography.

Chapter 5 Lavers, J. L. and Jones, I. L. 2007. Impacts of intraspecific kleptoparasitism and diet shifts on Razorbill *Alca torda* productivity at the Gannet Islands, Labrador. ***Marine Ornithology***

Chapter 6 Lavers, J. L., Jones, I. L., Robertson, G. J., and Diamond, A. W. Population dynamics of the Razorbill *Alca torda* in Atlantic Canada in relation to hunting bycatch and fox predation.

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This project was also made possible by the collaboration of several groups: Atlantic Cooperative Wildlife Ecology Research Network (ACWERN) and Canadian Wildlife Service as well as LabSea Charter Service (Capt. Randy Cahill) and Bold Coast Charter Co. (Capt. Andy Patterson) who provided professional logistical support that was critical to the research at several of my study sites. I would also like to thank my friends in Cartwright, Labrador whose friendship and support made my time in Labrador unforgettable, Les and Dora Hamel, Koko and Bonnie Hamel, and Tony Elson. Funding for this project was generously provided by ACWERN, the Canadian Wildlife Federation, Northern Scientific Training Program (Government of Canada), and The Seabird Group.

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My time here in Newfoundland has forever changed me. I arrived in 2003 a young, naïve, inexperienced researcher. Today I leave a determined and occasionally opinionated Ph.D. who refused to give up on a dream. This transformation is undeniably linked to the people in my life who, over the last four years, encouraged me to think critically, judge wisely, and work efficiently. Thank you to my committee members, Bill Montevecchi, Ted Miller, and Greg Robertson and co-author Tony Diamond.

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*"You're never in the gutter with your eyes on the stars"*

- Barlow

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## LIST OF ABBREVIATIONS AND SYMBOLS

| | |
|---|---|
| ACWERN | Atlantic Cooperative Wildlife Ecology Research Network |
| AICc | Akaike's Information Criterion |
| CMR | Capture-mark-recapture/resight |
| *Fa* | Fecundity |
| MR | Matinicus Rock |
| MSI | Machias Seal Island |
| *p* | Recapture probability |
| PMI | Petit Manan Island |
| PVA | Population viability analysis |
| QAICc | Quasi-Akaike's Information Criterion |
| *Sa* | Adult survival |
| SI | Seal Island |
| *Sp* | Pre-breeder survival (age 0-2 years) |
| $\Phi$ | Survival rate |
| $\lambda$ | Population growth rate |

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# CHAPTER ONE

# INTRODUCTION AND OVERVIEW

In this dissertation I report on the demography and other aspects of population biology of a long-lived seabird, the Razorbill *Alca torda*, in relation to a number of sources of natural and anthropogenic mortality. I also provide a critique of marking and sampling methods commonly used in capture-mark-recapture/resight (CMR) studies. My objectives were to provide accurate estimates of demographic parameters for Razorbills at various locations throughout their breeding range and to investigate the biological implications of these estimates. Parameters of interest were adult and pre-breeder survival, dispersal, natal philopatry, and productivity.

Many results of this thesis are applicable to long-lived organisms in general. To make this and other aspects of this thesis available to a non-specialist audience, I expand on several topics. This is followed by a brief summary of Razorbill biology, a detailed description of the study sites, outline of the specific goals and approaches of my study, and overview of the thesis chapters.

## 1.1. BACKGROUND INFORMATION

### *1.1.1. Demography and life-history of seabirds*

The term seabird has been applied to many species that exhibit a range of life-history traits. In its strictest usage, a seabird refers to members of the order Charadriiformes, Pelecaniformes, Procellariiformes, or Sphenisciformes that live and feed exclusively at sea, returning to land only to breed (Furness and Monaghan 1987). Several groups within these orders do not fit within this

strict definition. Many seaducks (Anatidae: Merginae) and cormorants (Phalacrocoracidae) breed inshore and rely on freshwater during the breeding season (Weimerskirch 2002). For the purposes of this review, only seabirds that depend primarily on marine resources will be discussed.

During the breeding season, most seabirds nest in large mixed-species colonies on inshore or offshore islands that are free of native mammalian predators (Lack 1968, 1972, Coulson 2002). As such, they have few or no anti-predator adaptations (Moors and Atkinson 1984). Nesting habitat varies greatly across species and can include earthen burrows (Lowther et al. 2002), rock crevices (Ainley et al. 2002), and cavities in trees (Gaston 1994). During the non-breeding season, most seabirds are found in offshore marine waters (Brown 1985, Durinck et al. 1993, Merkel et al. 1999).

Seabirds share many life-history characteristics, including small clutch size, delayed breeding, high adult survival, and long lifespan (Furness and Monaghan 1987). Most seabirds lay only a single egg annually and egg replacement is rare (Astheimer and Grau 1990). Most seabirds begin to breed between two and five years of age, however, large auks may not breed until age seven and some albatross species delay breeding for up to nine years (Ainley et al. 2002, Weimerskirch 2002). A long pre-breeding period is thought to be related to the reduced foraging ability of younger individuals coupled with the high cost of breeding (Lack 1968, Hudson 1985). In general, seabirds that delay their breeding only a few years tend to exhibit lower survival rates than those that delay for five or more years (Hudson 1985). For example, in the Alcidae, the Ancient Murrelet *Synthliboramphus antiquus* has one of the lowest survival rates and

commences breeding at only three years of age (Gaston 1994) whereas the Atlantic Puffin *Fratercula arctica* has one of the highest survival rates and delays breeding for five or more years (Petersen 1976, Lowther 2002). Life span in seabirds typically ranges between five and 25 years; however, fulmars and albatross can live for 50 years or more (Botkin and Miller 1974, Dunnet and Ollason 1978).

In long-lived seabirds, fecundity is at a minimum due to small clutch size and delayed breeding (Weimerskirch 2002); therefore seabirds rely heavily on survivorship of breeding adults to maintain population numbers (Croxall and Rothery 1991). Using the life expectancy (LE) estimator formula $LE = -1/\ln(\Phi)$, where $\Phi$ = annual survival, we can observe the changes in life expectancy as a result of changes in the survival rate (Lack 1954). For example, an adult Razorbill with $\Phi = 0.92$ (Steventon 1979) will live to 28 years of age while an adult with $\Phi = 0.90$ would be expected to live 22 years (Chapdelaine 1997). Therefore, small changes in the adult survival rate greatly influence the growth of a population by reducing both the lifespan and potential reproductive output of breeding adults. As a result, accurately quantifying adult survival is of critical conservation concern.

The growth and distribution of a population is also influenced by dispersal. In seabirds, established breeders generally exhibit strong site fidelity, but factors such as reproductive failure and disturbance may cause divorce of pairs, or dispersal of one or both members of the pair (breeding dispersal, Choudhury 1995, Greenwood and Harvey 1982). Dispersal of juveniles and fidelity to the breeding site (philopatry) is often treated separately from adult dispersal because juveniles tend to disperse over larger distances and may occupy different regions than adults

(including newly founded colony sites; Birkhead 1974, Greenwood and Harvey 1982, Harris 1983, Olsson et al. 1999). Due to the high cost and logistical challenges of following birds, the dispersal behavior of most seabird species is poorly known (Weimerskirch 2002). However, band recoveries, resightings, and new information from GPS and geo-loggers have provided insight into the movement patterns of individuals.

*1.2.1. Natural and anthropogenic sources of mortality*

Once a seabird reaches maturity, the rate of natural mortality is low (usually less than 10%; Weimerskirch et al. 2001). In contrast, some seabirds experience significant human related mortality through oiling, hunting, and entanglement in fishing gear (Furness 1984, Clark 1985, Denlinger and Kenton 2001, Croxall et al. 2002). Mortality is typically divided into two types, compensatory or additive. Using hunting as an example, the compensatory mortality hypothesis states that hunting mortality is compensated by changes in non-harvest, density-dependent mortality factors so that total (net) mortality does not increase (Nichols 1991, Williams et al. 2002). In contrast, the additive mortality hypothesis states that any increase in hunting mortality results in a proportional increase in total mortality. Numerous studies on waterfowl and seabirds have determined that mortality from hunting and oiling can be additive, and has been linked to population declines (Piatt and Naslund 1995, Sauer et al. 1990, Gauthier et al. 2001, Votier et al. 2005).

It is important to consider these issues from the point of view of population dynamics of seabirds and determine whether or not the observed mortality is substantial and additive relative to natural mortality. Monitoring seabird populations, estimating their demographic parameters, and

quantifying anthropogenic mortality, therefore form the basis of conservation and management directives, and are the fundamental issues addressed in this dissertation. In the following paragraphs I briefly review some of the current threats to seabirds that are addressed in the chapters of this dissertation.

*1.2.2. Harvest of seabirds*

Seabirds worldwide have been hunted for commercial and subsistence purposes for hundreds of years (Tuck 1961, Nettleship 1977, Blanchard 1984, Tasker and Becker 1992, Lyver 2000). The importance of seabird meat and eggs to local communities is well documented in Iceland (Nettleship and Evans 1985), on the Faeroe Islands (**Salomensen 1970**), Greenland (Christensen 2001), Newfoundland and Labrador (Nettleship and Evans 1985, Elliot 1991), and along the Quebec north shore (Blanchard 1983). The harvest of seabirds holds both traditional and recreational value. For example, in the Faeroe Islands, hunting is a summer event for many local communities, and in Newfoundland, murre hunting is done out of both necessity and sport (Piatt and Reddin 1984). In some cases, overexploitation has caused severe depletion, extirpation, and even extinction of seabird populations (Brooke 2004). For example, intense hunting of the Great Auk *Pinguinus impennis* led to its extinction in 1844 (Montevecchi and Kirk 1996).

Many seabirds are now protected from direct exploitation through the Migratory Birds Convention Act in Canada (Chardine et al. 1999) and the Migratory Birds Act in the United States (Boersma et al. 2002). However, traditional and recreational hunting of seabirds (in addition to poaching) continues throughout the world (e.g. muttonbirding in the Southern Ocean; Lyver and Moller 1999, Lyver 2000) and recent societal changes such as the rapid growth of the

human population and availability of modern tools such as guns and powerboats may increase the risk of overexploitation (Falk and Durinck 1992). With proper management, a few seabird populations have been harvested sustainably for generations and populations do not seem to be at risk (Skira 1985, 1986). However, for some seabirds, monitoring of the hunt and population growth is minimal or non-existent and it is not clear whether the hunt is sustainable. Chapter 6 of this dissertation will address the latter situation.

### *1.2.3. Fisheries bycatch*

Seabird bycatch (accidental capture of non target species) is a significant issue in many of the world's fisheries (Evans and Nettleship 1985, Lewison and Crowder 2002). In some cases, the endangered status of the species and considerable numbers caught in commercial fisheries has caused alarm among wildlife managers (Baker and Wise 2005). In response to this problem, several conferences and agreements have been developed, including the Kyoto Declaration (1995) and the United Nations Food and Agriculture Organization Code of Conduct for Responsible Fisheries (Garcia 2000). More recently, the United States Senate passed the Magnuson-Stevens Fishery Conservation and Management Act for 2006 (s.2012), which established strict limits on acceptable levels of bycatch and encourages the development of seabird bycatch compensatory mitigation techniques.

For many species, the legislation and mitigation methods imposed have proven to be successful in reducing bycatch of seabirds. However, in some cases, mitigation methods have not eliminated mortality or reduced it to a point that the population is sustainable (The Action Plan for Australian Birds 2000). For example, mitigation techniques used in the Eastern Tuna and

Billfish (ETBF) and Patagonian toothfish fishery have not reduced Flesh-footed Shearwater *Puffinus carneipes* or White-chinned Petrel *Procellaria aequinoctialis* mortality to a sustainable level, and with both species in decline, closure of the fisheries is likely (Bass and Clemens 2005, Priddel et al. 2006). A further concern is the considerable seabird bycatch that occurs in illegal fisheries outside the control of any national or international management plans (Gandini and Frere 2006).

*1.2.4. Climate change*

Seabird populations worldwide are experiencing extraordinary rates of environmental change including rapidly increasing sea-surface temperatures and decreasing ice coverage (Cane et al. 1997, Petrie et al. 2004). Climate change can affect seabirds indirectly through changes to their food supply or directly through severe weather events (Schreiber 2002). Numerous studies have documented effects of climate change on the timing and success of breeding in seabirds (Kitaysky and Golubova 2000, Quillfeldt 2001, Weimerskirch et al. 2001, Gjerdrum et al. 2003), but until recently, few studies have examined its effect on survival. It has been assumed that only short-lived species exhibit decreased adult survival in variable environments, because long-lived birds can move to more favorable waters when conditions are unfavorable (Schreiber and Burger 2001). However, this is not always the case. Modeling techniques now allow researchers to incorporate environmental variability in survival analyses and a number of recent studies have found that the amount of variation in survival explained by environmental variables in the model was high (Jones et al. 2002, Jones et al. *in press*, Sandvik et al. 2004). Through the development of these models we can better understand the effects of climate and predict the conditions seabirds will face in the future.

### *1.2.5. Native mammalian predators*

Predators of seabirds include ravens, rats and other seabirds (Phillips et al. 1999). In northern circumpolar regions, the Arctic fox *Alopex lagopus* is a common predator of ground-nesting birds (Bailey 1992, Elmhagen et al. 2000) and has been known to take eggs, chicks, and breeding adults (Birkhead and Nettleship 1995, Petersen 1982). The fact that so many seabird species nest on remote islands, on inaccessible cliffs and in burrows is considered to be a direct consequence of predator disturbance (Larson 1960, Tuck 1961, Williams et al. 2003).

Many bird populations seem able to withstand high rates of egg predation by foxes and few studies have conclusively linked population declines with native predators (Larson 1960, Paine et al. 1990). Seabirds seem to be the exception with reports of thousands of birds being killed and entire colonies abandoned (Petersen 1982, Southern et al. 1985, Thompson et al. 1998). In cases where native fox predation has been directly linked to declines in seabirds, foxes have been removed from islands and seabird populations have recovered (Petersen 1982). However, removal of native predators to protect birds poses an ethical issue since foxes represent a natural part of the environment (Cote and Sutherland 1997). Alternative techniques to exclude or limit the access of predators to seabird colonies such as translocations and fencing have been met with limited success (Forster 1975, Cunningham 1996, Viksne 1997), and predator removal in many cases remains the most effective method.

## 1.3. RAZORBILL SPECIES ACCOUNT

### *1.3.1. Population size and classification*

The Razorbill is the least abundant auk in North America with an estimated total population of less than 38,000 breeding pairs (Chapdelaine et al. 2001, Hipfner and Chapdelaine 2002). The global population is estimated at less than a million pairs (Chapdelaine et al. 2001), about half of which (~450,000 breeding pairs, Anker-Nilssen et al. 2000) breed in Iceland. Two subspecies are recognized, the larger *A. t. torda* in northern Europe, and the smaller *A. t. islandica* of North America (Cramp et al. 1985).

### *1.3.2. Breeding habitat and phenology*

Razorbill populations in the western Atlantic range from Greenland to the Gulf of Maine during the breeding season, and south to North Carolina during winter (Hipfner and Chapdelaine 2002). Breeding colonies are almost exclusively on offshore islands where Razorbills occupy nests in low-lying boulder scree as well as ledges and crevices on cliffs (Gaston and Jones 1998, Hipfner and Chapdelaine 2002). In North America, arrival of birds on the breeding site occurs in late April to early May. Razorbills incubate their eggs for up to 38 days (Hipfner and Bryant 1999). Chicks grow quickly and leave the nest at approximately 18 days of age, accompanied by and remaining with the father in open waters for up to two months (Hope Jones and Rees 1985).

### *1.3.3. Status, trends, and conservation concerns*

Estimating Razorbill populations has proven difficult because most birds nest in enclosed sites that are not easily visible to researchers (Hipfner and Chapdelaine 2002). In addition, many colonies in Labrador, Iceland, and Norway have not been surveyed in more than 20 years (Anker-Nilssen et al. 2000, Chapdelaine et al. 2001). Population trends are known for a few well-studied colonies, however global or regional changes remain difficult to detect.

Razorbills were hunted extensively up to the early 1900s resulting in large population declines on both sides of the Atlantic Ocean (Anker-Nilssen et al. 2000, Chapdelaine et al. 2001). In Britain and Norway, some Razorbill populations declined steadily from 1960-1990 (Anker-Nilssen et al. 2000), likely due to mortality in the commercial gill net fisheries. In North America, Razorbill populations in Newfoundland and Quebec declined historically as a result of unregulated hunting and gill-net mortality (Chapdelaine et al. 2001, Robertson and Elliot 2002). In the Gulf of St. Lawrence, declines in Razorbill populations were recorded as recently as 1983 (Chapdelaine and Laporte 1982). Since 1917, Razorbills are protected in Canada and the United States under the Migratory Birds Convention Act (Hipfner and Chapdelaine 2002) and, although some populations appeared to be increasing in recent years (Robertson et al. 2002), multiple years of low productivity and survivorship at the largest colony, the Gannet Islands, is of conservation concern (see Chapters 4 to 6).

## 1.4. STUDY SITES

### *1.4.1. Gannet Islands, Labrador*

This study was conducted primarily at the Gannet Islands, Labrador, Canada (53°56'N, 56°30'W; Figure 1.1). The Gannet Islands includes six treeless islands (GC1-GC6, Figure 1.2) located approximately 40 kilometers northeast of Cartwright, Labrador. The Gannet Islands are legally protected as a provincial Ecological Reserve and support the largest colony of Razorbills in North America (~ 9,800 breeding pairs; Chapdelaine et al. 1999, 2001). In the 1980s, the climate at the Gannet Islands was typical of the sub-Arctic region with heavy pack ice remaining around the islands until late June (Birkhead and Nettleship 1983). However, the area has

experienced substantial warming in recent years, and the water surrounding the islands has recently been clear of ice as early as the first week of May (Canadian Ice Service 2006).

### *1.4.2. Machias Seal Island, New Brunswick*

Additional demographic data for Razorbills were collected on Machias Seal Island (MSI hereafter), Bay of Fundy, New Brunswick (44°3'N, 67°06'W; Figure 1.2) through a collaborative effort with Dr. Antony Diamond of the University of New Brunswick. MSI is a small (9.5 ha) treeless island ~10 km off the coast of Maine (Diamond and Devlin 2003). It is a Migratory Bird Sanctuary owned by the Canadian Coastguard and managed by the Canadian Wildlife Service of Environment Canada. Approximately 543 Razorbill breeding pairs nest on the island (Chapdelaine et al. 2001).

### *1.4.3. Gull Island, Newfoundland*

Reproductive data were collected on Gull Island, Newfoundland (47°15'N, 52°46''W, Figure 1.2) through a collaborative effort with Dr. Greg Robertson of the Canadian Wildlife Service. Gull Island is one of four islands in the Witless Bay Ecological Reserve. Currently ~ 261 Razorbill pairs breed on the island (Chapdelaine et al. 2001).

### *1.4.4. Herring Islands, Labrador*

Data on short-distance dispersal were collected in July 2005 through resightings of Razorbills banded as chicks on the Gannet Islands that are now breeding on the Herring Islands, Labrador (54°19'N, 57°5'W; Figure 1.2). The Herring Islands include three small islands located ~60 km north of the Gannet Islands. The Herring Islands are home to ~1,800 Razorbill pairs and

represent one of the most northerly and least studied Razorbill colonies in Canada (Chapdelaine et al. 2001).

## 1.5. APPROACHES TO THIS STUDY

### *1.5.1. Capture-Mark-Recapture/Resight data and models*

The estimation of demographic parameters forms the basis of all wildlife population studies and involves the collection of large amounts of data and utilization of precise methods to analyze these data (Danchin 1992). Capture-mark-recapture/resight (CMR) studies are frequently used to identify long-term trends in survival, productivity, or behavior of marked individuals. CMR involves marking, releasing, and resighting individuals on two or more occasions (Lebreton et al. 1992). The use of simple marking techniques to follow individuals over time dates back to the 1930s (Lebreton et al. 1992). However, the popularity of CMR has greatly increased over the last 60 years following the development of software that is capable of handling large, complex data sets (Cormack 1964, Jolly 1965, Seber 1965, White and Burnham 1999).

Four assumptions common to most CMR models are: (1) all marked animals in the population immediately following the sampling period $i$ have the same probability of surviving to the sampling period $i$+1; (2) all marked animals at sampling period $i$ have the same probability of being recaptured or resighted; (3) marks are neither lost nor overlooked and are recorded correctly; and (4) marks do not affect the animals behavior or survival probability (Seber 1982, Pollock et al. 1990). Violation of any of these assumptions can result in biased estimates. For example, violation of the second assumption is common for studies involving species that do not exhibit site fidelity, moving outside the sampling area where they are not available for recapture.

Another consideration when developing CMR studies for seabirds is the life span of the species. In long-lived birds, demographic parameters vary naturally from year to year as a result of individual and environmental differences (Gould and Nichols 1998). To account for this, researchers must sample populations over many years before trends in the response of an organism to perturbations become detectable.

*1.5.2. Population viability analyses and model development*

In addition to quantifying demographic parameters, an important goal of wildlife conservation studies is to identify populations that are declining, and to determine what can be done to stabilize the population (Reed et al. 1998). To predict the fate of populations, researchers commonly use a technique known as population viability analysis (PVA; Hamilton and Moller 1995, Brook and Kikkawa 1998, Reed et al. 1998, Jones 2002). The use of PVA in wildlife conservation has received criticism regarding uncertainty in estimating extinction risk (Brook et al. 2000, Coulson et al. 2001, Ellner et al. 2002, Reed et al. 2002). Therefore, PVA analysis is typically used only as a guide to test the efficiency of different management scenarios (Hamilton and Moller 1995).

Perturbation analysis is a technique commonly used to identify demographic parameters that are most important to the asymptotic properties of the population growth rate, lambda ($\lambda$, Morris and Doak 2002). Two types of perturbation analysis are (1) sensitivity analysis which determines how sensitive one parameter is to a change in another, and (2) elasticity analysis which is used to determine the relative importance of parameter that influence the population growth rate (Morris and Doak 2002). Elasticity analysis, therefore, identifies key parameters that are most important

for species conservation (Jones 2002) and will be used in this study to guide management plans with regards to Arctic fox predation and other mortality sources.

## 1.6. PURPOSE AND GOALS OF STUDY

### *1.6.1. Conceptual framework*

The life-history parameters of seabirds constitute a strategy which evolved as a result of adaptive responses accumulated over time (Wilbur et al. 1974). Unfortunately for seabirds, human populations are increasing rapidly and changes to the environment as a result of anthropogenic activities occur at a rate faster than many species can adjust to. Seabirds have low potential for recovery built into their breeding biology (Russell 1999), therefore understanding the threats to seabird populations and how they respond to change is essential for proper management and protection.

### *1.6.2. Study rationale*

Most demographic studies involve monitoring a single local population for a few years, often less than the life span of the focal species. For many species, the *only* available data are from local, short-term studies, and the results (i.e. annual survival estimates) are often assumed to be similar for other nearby populations. In contrast, long-term, multi-site studies are rare (Wooller et al. 1992), but are particularly important as they enable the scale and pattern of natural variability to be understood and unusual or atypical responses to be identified (Micol and Jouventin 2001). The data presented in my study were collected over 12 years (1995-2006) on four islands that encompass almost the entire North American breeding range of the focal species, the Razorbill.

The Razorbill was chosen as the study species for this project because of its small population size, restricted geographical range, and sensitivity to human activities. In addition, the data sets available for Razorbill were large and spanned many years, making them appropriate for a demographic study. Furthermore, the literature on Razorbills suffers from a lack of recent studies, especially on the threats to populations. For example, in the 1980s, a number of studies concluded that combined annual mortality from oiling, hunting, and fisheries bycatch likely exceeded 15% and was not sustainable (Piatt and Nettleship 1987). Mortality may now be lower due to a reduction in fisheries bycatch following the moratorium in 1992 (see above); however no studies have addressed this or other issues (i.e. hunting mortality) in the last 20 years. My project was developed to address these data gaps, utilizing recent data on hunting bycatch and predation to develop a comprehensive population model for Razorbills. In natural environments, mortality factors do not occur independently of one another, therefore it was necessary to develop a model which could incorporate multiple factors that can vary naturally over time in response to current conditions. This model is presented in Chapter 6.

## 1.7. OVERVIEW OF CHAPTERS

A primary goal of this dissertation was to provide estimates of age-specific survival for juvenile and adult Razorbills on the Gannet Islands and MSI. However, following my first field season in 2003, a number of band resighting errors were detected at both study sites, which prompted me to develop and implement techniques to quantify the error and find ways to minimize bias in survival estimates. Key issues identified were (1) are the survival estimates produced as a result of CMR studies reliable, (2) which techniques should be used to minimize bias, and (3) what

effect will bias in the survival estimate have on the development of conservation programs? These analyses are reported in Chapter 2 "The effects of band resighting error on survival estimation in Razorbills (*Alca torda*) with implications for other bird studies".

In Chapter 3, "Natal and breeding dispersal of Razorbill (*Alca torda*) in Atlantic Canada", we introduce another issue common to CMR studies: dispersal of marked individuals outside the sampling area. Dispersal violates a key assumption of Cormack-Jolly-Seber CMR models, which assume that every marked animal present in the population during a sampling period has the same probability of being recaptured or resighted. This chapter reports on observations of long- and short-distance dispersal events in Razorbill through resighting of birds banded throughout eastern Canada and the United States. The objectives of this chapter were to (1) establish which environmental and ecological factors may be responsible for the observed pattern of movement, and (2) discuss the consequences of dispersal in relation to the assumptions of the CMR survival analyses presented in Chapter 4.

In Chapter 4 "Annual survival of Atlantic Canadian Razorbills (*Alca torda*) varies with climate and oceanography" I present CMR models to estimate adult and pre-breeder survival for Razorbills, which incorporate a number of recommendations made in Chapters 2 and 3. The objectives of Chapter 4 are to (1) determine if demographic parameters of Razorbills in Atlantic Canada are sufficient to indicate a stable or increasing population, and (2) detect whether large-scale variation in climate and oceanography influences over-winter survival of Razorbills. Results of CMR analysis using data from 1995-2006 for more than 2000 known-age individuals banded as chicks and 500 birds banded as breeding adults are presented.

Chapter 5 "Impacts of intraspecific kleptoparasitism and diet shifts on Razorbill *Alca torda* productivity at the Gannet Islands, Labrador" reports on changes in the diet of Razorbill chicks over the last 26 years in relation to recent observations of high rates of intraspecific kleptoparasitism and low productivity in Razorbills on the Gannet Islands. I discuss how increasing sea surface and air temperatures along with the disappearance of pack ice during the breeding season may explain my observations. I compare Razorbill productivity on the Gannet Islands to past and present studies and discuss the implications of multiple years of low productivity on long-term population dynamics. Prior to submission of this dissertation to the School of Graduate Studies, Chapter 5 was submitted to Marine Ornithology for publication.

In Chapter 6 "Population dynamics of the Razorbill *Alca torda* in Atlantic Canada in relation to hunting bycatch and fox predation" I use the demographic parameters estimated in the preceding chapters to develop a model to project the Gannet Islands and MSI Razorbill populations 20 years ahead and visualize the population trends if current conditions persist. This study presented a unique opportunity to examine the effects of native mammal predation and hunting bycatch through comparing population trends at an affected (Gannet Islands) and unaffected (Machias Seal Island) population. Recommendations for the conservation and protection of Razorbills are discussed.

In Chapter 7 I summarize the significance and implications of the results from Chapters 2-6 for Razorbills and other long-lived seabirds. I emphasize the importance of long-term, multi-site studies and contribution of this study to our understanding of the variation in seabird life-history

parameters across their range and in relation to environmental variability and human activities. In addition, recommendations for managers on how to increase Razorbill reproductive success and juvenile survival rates are discussed.

Figure 1.1. Map of the Gannet Islands, Labrador showing the location of the six islands in the cluster.

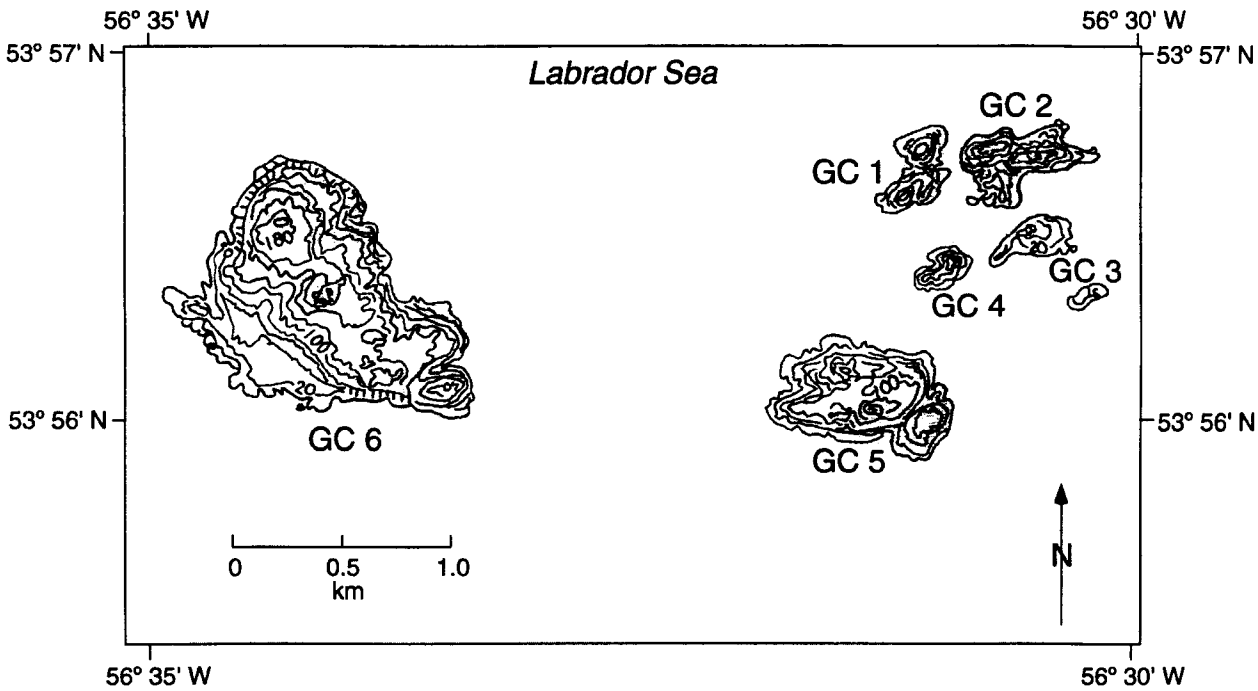
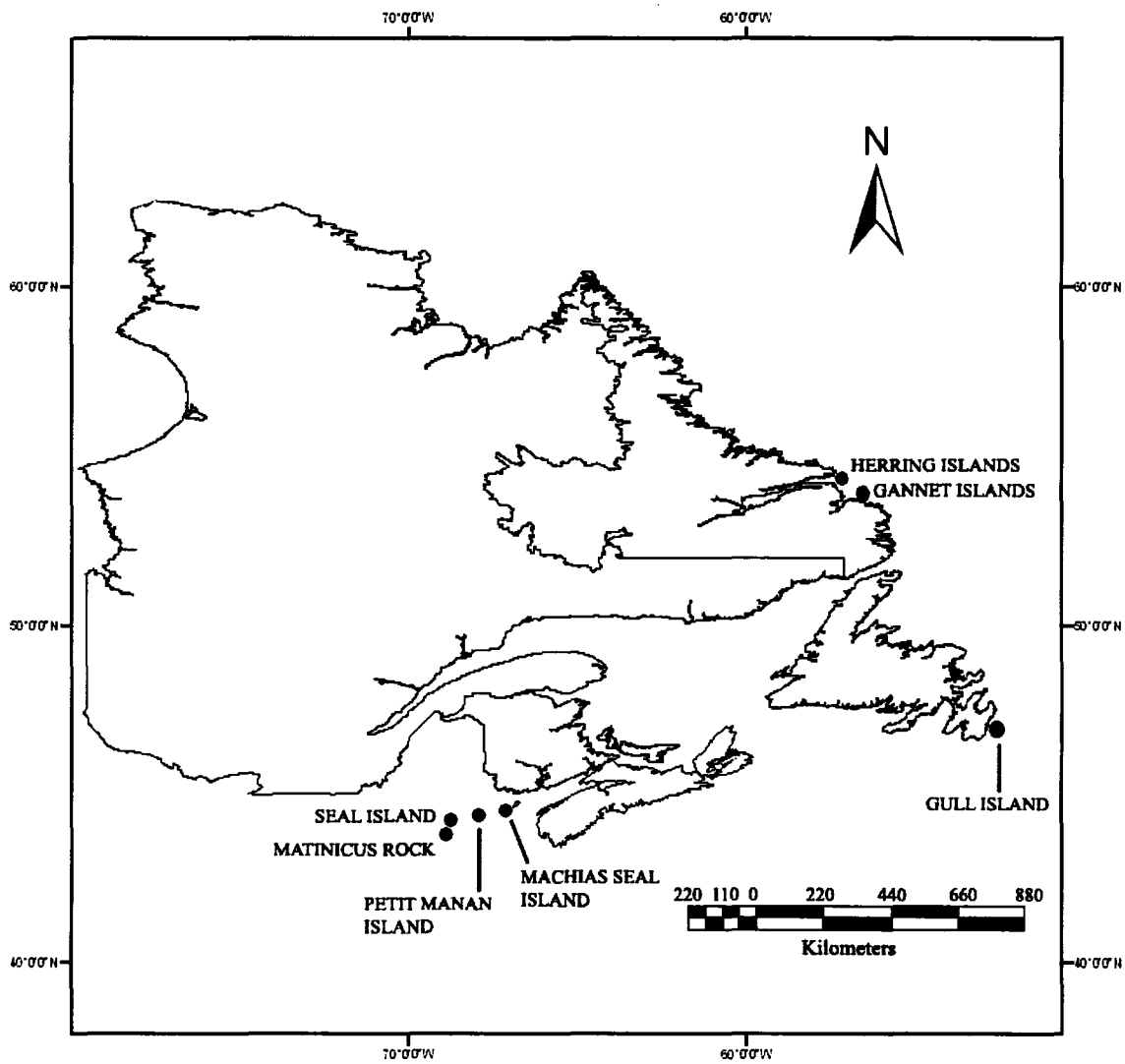


Figure 1.2. Map of the study locations.



# CHAPTER TWO

# THE EFFECTS OF BAND RESIGHTING ERROR ON SURVIVAL ESTIMATION IN RAZORBILLS (*ALCA TORDA*) WITH IMPLICATIONS FOR OTHER BIRD STUDIES

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## 1.1. ABSTRACT

Visual markers are frequently used in wildlife studies to identify individual animals. These markers are useful since identification can be made without recapture, thus minimizing disturbance. However, studies have shown that errors associated with reading and recording markers adversely influence the estimation of population parameters. Here, using the example of triangular field-readable leg bands on Razorbill *Alca torda*, we report on a simple experimental protocol for quantifying band resighting error rates, and for identifying trends in misreading of band numbers. The resighting error rate varied from $0.035 \pm 0.012$ to $0.134 \pm 0.018$ depending on observer distance and conditions under which the bands were read. Misidentification of the digits five and six accounted for more than 48% of all errors. Ninety-four percent of all incorrectly read bands correctly corresponded to a valid entry in the banding data base, likely due to the fact that more than 9000 Razorbills have been banded with similar markers over the last 12 years. The effect of band resighting error on survival estimation is discussed and recommendations to reduce error in resighting bands are provided.

## 2.1. INTRODUCTION

The use of capture-mark-recapture/resight (CMR) techniques in wildlife studies has presented numerous challenges including the loss of or damage to bands, especially in long-lived species (Austin 1957, Lloyd and Perrins 1977, Lyngs 2006). A key component of CMR survival models is the adherence of the data to model assumptions, two of which are that tags are not lost and individuals remain equally identifiable (Anderson et al. 1985). Band wear and loss clearly violate these assumptions and as a result, have received much attention in the literature (Nisbet and Hatch 1983, Wiebe et al. 2000, Jovani and Tella 2005, Breton et al. 2006b). An equally serious violation however, referred to here as resighting error (resulting from misreading of one or more of the inscribed digits on a 'field readable' band), has rarely been addressed and is therefore the focus of this study.

For most long-lived animals, survival of breeding adults is a crucial parameter (Pfister 1998, Saether and Bakke 2000); so its accurate estimation is of critical importance. In seabirds, large amounts of data can be collected with minimal disturbance to the colony through the resighting of marked individuals, therefore this technique has become widely used (Lebreton 2001). However, errors associated with reading and recording of band combinations are not uncommon and have been shown to influence the estimation of population parameters (Atkinson et al. 2001, Schwarz and Stobo 1999, Weiss et al. 1991).

Recent advances have been made in modeling to incorporate factors such as band loss and band wear into survival analyses (Conn et al. 2004, Schwarz and Stobo 1999). Here we present a case study using band resighting error rates for Razorbills *Alca torda* to show the effect of incorrect

band readings on survival parameter estimation. The objectives of this study were to 1) evaluate the effects of resighting errors on survival estimates obtained for Razorbills breeding at the Gannet Islands, Labrador, (2) identify factors associated with resighting errors including distance and digits used, and (3) make recommendations on methods that may reduce resighting error in future studies.

## 3.1. METHODS

### *3.1.1. Study sites*

The primary field study site for this project was the Gannet Islands, Labrador, Canada (53°56'N, 56°30'W), which include six islands (GC1-GC6) located in the Atlantic Ocean, approximately 40 kilometers northeast of Cartwright, Labrador. The Gannet Islands support the largest colony of Razorbills in North America with approximately 9,800 breeding pairs (Chapdelaine et al. 2001). Banding of Razorbill adults and chicks began in 1996 and more than 5500 birds have been banded to date. Additional data (experimental protocol only, see below) were collected on Machias Seal Island, New Brunswick, Canada (44°3'N, 67°06'W) and Tern Island, Hawaii (23°45'N, 166°10'W).

### *3.1.2. Band structure and combinations in use*

Captured Razorbills were banded with size 5 triangular, stainless steel, field readable leg bands produced by Porzana Ltd (see Lloyd and Perrins 1977 and Lyngs 2006 for a detailed description; Figure 2.1). This style of band was originally designed by the British Trust for Ornithology in the 1980s to minimize wear of the digits in the band code in species such as the Common Murre *Uria aalge* that damage their bands when the tarsus is in contact with the ground (Harris and

Rothery 2004). This design was recently adopted for use on Razorbills. Bands were engraved with a three-digit prefix and a five-digit suffix. The size of the prefix digits (1 mm in height) are such that they can not be reliably read with a spotting scope at distances of more than 7-10 meters under ideal conditions and for the purposes of this study, were not included in the analyses. The five digit suffix consists of stamped numbers 4 mm high (Figure 2.1) and could be reliably read with a spotting scope at distances of up to 15-20 meters.

Bands are typically issued by the Canadian Wildlife Service in bundles of 50 or 100 and researchers can request 1000 bands or more per year. Currently no measures are in place to ensure that different banding locations receive band series that are significantly different from other sites (e.g. all Razorbill bands have an 895 prefix and until 2006, all band suffixes began with the digit 1). For example, band strings 895-14001 to 14300 were used on Machias Seal Island and bands 895-14301 to 14500 were used on the Gannet Islands (Table 2.1). To date, more than 10,000 Razorbills have been banded (most as chicks) in Atlantic Canada and Quebec.

*3.1.3. Weather and participant data*

The date and time during which all experiments were conducted were carefully selected to ensure consistent weather and lighting conditions. Weather data recorded included percent cloud cover, wind velocity and direction, and temperature. Experiments were conducted over five days during May 2005 and July 2006 when observed wind speed was less than 10 km/hr and cloud cover was below 20%. Participants were asked to provide information on the number of months or years during which they had experience resighting birds and the type (i.e. color versus metal) and size of bands resighted.

*3.1.4. Natural conditions protocol*

Two participants at a time were asked to read band numbers on up to 30 marked Razorbills in the field from a blind on the Gannet Islands using a Swarowski STS-80 HD spotting scope. All bands were read using 20x magnification. Razorbills were located no more than 15 meters from the front of the blind. Each participant was given five seconds to view the band through the scope and then record the band number in private. Participants were asked to rank each resighting according to the following reliability scale: (1) excellent resighting, participant was 100% confident they accurately read and recorded the band number, (2) good resighting, participant was >95% sure they accurately recorded the band number, however, in a natural setting, would have elected to follow the bird for a longer period of time, and (3) poor resighting, participant was unsure of one or more digits in the band number. Participants were then given time to make any additional comments including justification for each ranking (e.g. reflection off the band, not enough lighting to view band, bird was in motion).

Resightings from both participants were compared and contradictory resighting events (i.e. the band number recorded by one participant did not match the other participant) were identified. Because it was normally possible to determine which recorded number was correct (or if both recorded numbers were incorrect), we developed an experimental protocol for which the correct band number was known.

*3.1.5. Controlled experimental protocol*

Twenty-five participants were asked to read 20 Razorbill bands (not attached to birds' legs) in carefully controlled conditions, at distances of 15 and 22 meters with the spotting scope set to

20x magnification. These distances were chosen as fifteen meters represents the typical conditions under which Razorbill resighting is conducted on the Gannet Islands whereas 22 meters is at or near the limit at which most researchers can reliably read bands. Therefore, we feel the error estimates generated from this study will represent the typical range of error that can be expected.

Since the probability of misreading a given band combination is not equal for all bands, all test bands were selected at random to minimize bias. The examiner recorded the correct band number and placed the band on a flat platform facing directly towards the participant. The participant was then given five seconds to observe and record the band number. Additional time between band viewings was given to allow participants time to provide a ranking (as described above) and any additional comments. The band numbers recorded by each participant were then compared to the known band numbers and incorrect resightings were identified.

*3.1.6. Statistical analyses*

Statistical analyses were conducted using JMP (SAS Institute Inc, 2005). Resightings that received a poor reliability ranking from the participant were excluded from analysis. Error rates were determined by calculating the number of bands or digits read incorrectly divided by the total number of bands or digits read. The number of errors and poor resights were calculated for each distance in the experimental protocol and statistical significance was determined using Pearson Chi-square Test (Sokal and Rohlf 2000). Trends in digits that were consistently read incorrectly were identified by calculating the error rate per digit (0 through 9) by dividing the

number of times the digit was misidentified by the total number of times the digit was available to be read (i.e. included in the band number being read by the participant).

## 4.1. RESULTS

### *4.1.1. Natural conditions band reading*

A total of 73 individual bands on Razorbills were read over 4 days at the Gannet Islands. Each band was read by at least two participants with 24 bands being resighted in two or more resighting periods. The total number of resightings was 228 (i.e., 114 events with a band read by two observers). Eight inconsistencies were identified giving an apparent error rate of 0.035 (SE = 0.012, n = 228; Appendix 2.1). There was no bias in the errors for a particular band combination with each of the eight errors occurring for eight different bands. Of the errors made, the most common involved the digits eight and nine, however, when considering the number of errors made per digit as a proportion of the total number of times the digit was available to be read (i.e., the digit may appear more than once on an individual band), the digits five and six accounted for the highest number of errors (error rate = 0.027 ± 0.019 and 0.018 ± 0.013).

### *4.1.2. Controlled experiment band-reading*

For each participant, 20 bands were selected at random from a set of 41 bands at 15 and 22 meters; therefore some bands were read twice by the same participant. Only four participants incorrectly read the same band twice (e.g. at both 15 and 22 meters) and variation in misreading rates for each band was small, ranging from 0.041± 0.03 to 0.136 ± 0.06.

At 15 meters a total of 406 resightings were recorded (excluding poor resightings) and 24 errors (20 single digit errors, 4 multiple digit errors) were identified generating an error rate of 0.059 ± 0.001. At 22 meters 356 resightings were recorded and 48 errors (45 single digit errors, 3 multiple digit errors) were identified for an error rate of 0.134 ± 0.018. Only four of the 72 incorrect band readings recorded by participants did not correspond to a valid band number in the database. Forty-five observations received a poor ranking by the participant at 15 meters and 108 at 22 meters. Overall, the number of incorrect resightings and poor rankings recorded at 22 meters were significantly greater than at 15 meters ($p < 0.001$, $\chi^2 = 12.71$). Observations which received a poor ranking accounted for 15.8% (n = 153) of all band readings.

The ten most commonly misidentified band digits are presented in Appendix 2.1. Overall, the digits five (n=17) and three (n=16) were the most frequently misidentified, accounting for more than 48% of all errors made. However, proportionately the digits five and six were read incorrectly at the highest frequency (error rate = 0.045± 0.012 and 0.051 ± 0.013 respectively) and zero was read incorrectly the fewest number of times (error rate = 0.004 ± 0.003).

## 5.1 DISCUSSION

Numerous studies have reported parameter estimates for a variety of species through the use of CMR techniques (see Lebreton et al. 1992 and Pollock 1991 for a review). However, only a few studies have examined the impacts of resighting error on survival estimation with somewhat conflicting results. For example, Weiss et al. (1991) found that 6.3% of resightings of neck banded Canada Geese (*Branta canadensis*) were incorrectly made after the bird was recaptured without a neck band or was harvested, however, this error was not found to significantly

influence the survival estimate. Schwarz and Stobo (1999) found that for branded gray seals *Halichoerus grypus*, incorrect resightings were infrequent and easily detected; therefore the survival estimate was only slightly inflated early in the study.

Resighting error rates were high and varied with observer distance in the experimental protocol (Table 2.3). However, like many studies conducted under a controlled setting, the experimental protocol likely provided a more challenging task for the observer than did conditions under which resighting would naturally occur. For example, the bands were held stationary and placed so that they were directly facing the participant. Under typical resighting conditions, Razorbills walk around allowing the observer to view the band from different angles, often providing lighting angles that maximize visibility of the bands' numbers. Furthermore the observer is not usually limited to five seconds observation time. Therefore we feel that the error rate reported for the experimental protocol may be an overestimate or 'worst case scenario'. We acknowledge these limitations and emphasize that the main purpose of this part of our experimental protocol was not to precisely estimate error in the field, but to identify trends in digit errors using known band numbers. Overall, we feel that the error rate calculated under natural conditions (Table 2.3) is probably closer to the amount of error generated when resighting live individuals and is comparable to the error rate reported by Weiss et al. (1991).

Trends in the misidentification of certain digits were identified with the most problematic digits being five and six. Weiss et al. (1991) reported distinct trends in the identification of certain characters used to code the neck bands and in contrast to our study, Weiss et al. (1991) found that the digit six had the lowest error rate. Initially we predicted that the digits three and eight

were the most likely to be confused given their similarity in structure. However, this combination of digits accounted for only 5% of the errors made.

The results of this study highlight a number of issues relating to the resighting and recording of band numbers. First, on two separate occasions, the participant appears to have correctly observed the band number presented to them but recorded the digits in the wrong order. Thus, errors in resighting data accumulated both from difficulties in observing as well as recording band numbers. Though infrequent and likely not a significant source of error for this study, we feel that this is a concern which must be addressed by researchers when training individuals to resight bands. Because dyslexia is a common condition, individuals need to be tested before being assigned complex band reading tasks. Second, since band numbers engraved on leg bands are not manufactured or distributed randomly, individuals banded at a common place or time have band numbers that often have many digits in common. Since researchers typically return to the same site multiple times, repeated observations of similar band numbers may lead to complacency. A final and perhaps more important issue is the fact that when one band is read incorrectly, two errors may be generated. This occurs when the band number resighted is misidentified or recorded incorrectly and the new number matches another banded individual. In this case, the bird resighted will not be recorded as present in the population and the bird that was not seen, but its band number recorded, will appear in the dataset. In this study, 94% of bands read incorrectly during the experimental protocol correctly corresponded to an existing band number in the database. This is likely the most troubling source of error as it is difficult to detect and quantify, especially when hundreds or thousands of individuals are banded.

In long-lived species, adult survival is the key parameter to which the population growth rate is the most sensitive (Lebreton and Clobert 1991) meaning that small deviations can have a huge impact on the status of a population. Band resighting error has the potential to seriously influence estimation of the survival rate; therefore it is essential to find a way to accurately incorporate resighting error into survival models. Since the size and type of band used along with the distances and conditions under which resighting is conducted vary greatly, the resighting error rate should be estimated for studies on an individual basis. In order to minimize error we make the following recommendations. Researchers should develop and implement their own resight ranking scheme as well as establish minimum criteria for the number of times an individual band number must be resighted before it is considered confirmed. In addition, researchers should avoid placing bands in series on individuals in the same location and attempt to avoid the use of the digits five and six where possible. The use of metal, auxillary bands with large digits in addition to the Federal band is a simple solution; however the cost and time required to place a second band on birds may be a challenge for studies involving thousands of birds. Another alternative would be for banders to only use some of the bands issued to them from the banding office. Through randomly selecting bands which are to be placed on birds and keeping the remaining bands in the lab, incorrect resightings can be more easily detected. Support for this idea comes from resighting data collected on Machias Seal Island where since 1998, 13 bands were reported as having been resighted in the field, but had not yet been placed on birds (J. Lavers, pers. obs).

Two final recommendations for band manufacturers involve the use of "Read Regular" fonts and check digits. Read Regular fonts have been developed for individuals with dyslexia and feature

improved readability (Frensch 2003). We recommend that the current fonts used on North American bird bands be replaced with Read Regular fonts. Another improvement would be the use of check digits, a form of redundancy check used for error detection consisting of a single digit computed from the other digits in the message (Kirtland 2000). Check digits have been widely used in Universal Product Codes and International Standard Book Numbers. Both these options may prove to be an effective (and easy) alternative for band manufacturers.

We were unable to address the issue of past resighting experience on the error rate due to small sample size; however, from a simple review of the data, it appears that participant experience is not correlated with their ability to correctly identify band numbers. Errors were detected for 21 of the 25 participants with multiple errors being made by individuals with little and extensive resighting experience. Future studies should conduct an in depth examination of the relationship between observer experience and resighting error rate.

ACKNOWLEDGEMENTS

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Figure 2.1. Example of a size five, triangular, field-readable Razorbill band used in this study.

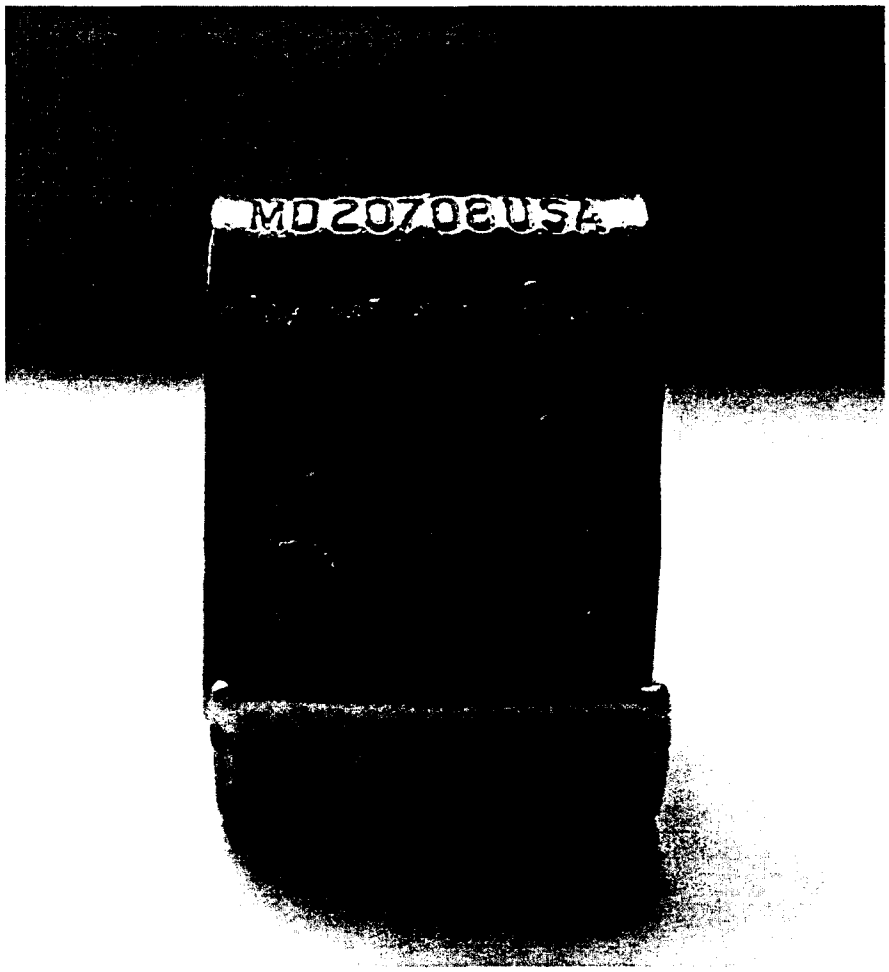

Table 2.1. Banding records for Razorbills in Atlantic Canada showing how different banding locations are issued bands in close series.

| Band number | | |
|---|---|---|
| From | To | Location used |
| 895-14001 | 895-14300 | Machias Seal Island, New Brunswick |
| 895-14301 | 895-14500 | Gannet Islands, Labrador |
| 895-14501 | 895-15105 | Gulf of St. Lawrence, Quebec |
| 895-16801 | 895-16825 | Hamilton Inlet, Labrador |
| 895-16826 | 895-16976 | Witless Bay, Newfoundland |

Appendix 2.1. Digits most frequently associated with resighting errors made under natural and experimental conditions.

| Digits Misidentified | Experimental Conditions 15 m | Experimental Conditions 22 m | Natural Conditions 15 m | Total |
|---|---|---|---|---|
| 1 for 7 | 0 | 3 | 1 | 4 |
| 7 for 1 | 0 | 4 | 0 | 4 |
| 3 for 5 | 1 | 2 | 1 | 4 |
| 5 for 3 | 1 | 2 | 0 | 3 |
| 3 for 6 | 0 | 2 | 0 | 2 |
| 6 for 3 | 2 | 2 | 0 | 4 |
| 3 for 8 | 0 | 1 | 0 | 1 |
| 8 for 3 | 0 | 2 | 0 | 2 |
| 5 for 6 | 3 | 5 | 0 | 8 |
| 6 for 5 | 0 | 3 | 1 | 4 |
| 5 for 9 | 0 | 0 | 1 | 1 |
| 9 for 5 | 1 | 1 | 0 | 2 |
| 8 for 9 | 2 | 2 | 1 | 5 |
| 9 for 8 | 2 | 0 | 1 | 3 |

# CHAPTER THREE

# NATAL AND BREEDING DISPERSAL OF RAZORBILLS (*ALCA TORDA*) IN EASTERN NORTH AMERICA

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## 1.1. ABSTRACT

Knowledge of the processes that drive local population dynamics, namely birth, death, immigration, and emigration are critical to conservation and management. Until recently, our understanding of the role of movement in animal populations was limited due to a prevalence of studies on single local populations. Here we report on local and regional movement patterns of Razorbill (*Alca torda*), the least numerous Atlantic alcid, through the use of multi-site capture-mark-recapture/resight for five breeding locations spanning their entire North American breeding range. Razorbill philopatry and breeding site fidelity rates for the Gannet Islands, Labrador were high with 83% of young birds (n = 340) and 97% of adults (n = 149) returning to the same colony to breed. The distance moved between the natal colony and the colony where an individual later bred was significantly greater for birds banded as chicks, both between colonies on the same island and within islands in the Gannet Islands cluster. Regional movements of 40 banded individuals were recorded during 2003-2006, including seven birds that were confirmed breeding at a location different from their natal colony. Emigration distances among colonies in North America ranged from 57 to 1737 km, providing an unexpectedly high rate of movement of birds between breeding colonies that has not been previously reported for any auk species. One bird, banded as a chick on Digges Island, Nunavut in 1982 was recaptured 24 years later as a breeder on the Gannet Islands (1737 km away). A chick banded on Handa Island, Scotland in 1971 was seen four times in 2004 at the Gannet Islands (3210 km away). Despite exhibiting low productivity and survivorship, Razorbill populations at some Atlantic Canada breeding sites have been increasing. We conclude that the dispersal and recruitment of individuals into new colonies that are characteristic of other seabird species may also partly explain patterns of population dynamics at North American Razorbill colonies.

## 2.1. INTRODUCTION

Wildlife population dynamics are the result of four key components, namely birth, death, emigration and immigration (Sutherland et al. 2002). For most seabirds, especially the family Alcidae, birth and death rates have been well studied, but less is known about immigration and emigration (Greenwood and Harvey 1982, van Noordwijk 1993, Gaston and Jones 1998, Joe and Pollock 2002, Brooke 2004). This lack of knowledge on seabird dispersal is often a result of logistical limitations posed by the large distances over which birds can disperse (Lindberg et al. 1998, Cam et al. 2004), and difficulty of identifying marked individuals in large colonies. Dispersal has the potential to contribute significantly to spatial and temporal variation in population size. In particular, whether individuals of long-lived colonial seabird species habitually breed at their natal colony or disperse to other colonies is a crucial decision that has far reaching implications for the monitoring and conservation of populations.

A number of seabird studies have recorded population growth far greater than can be explained by the species biology (Leslie 1966, Hilden and Pahtamaa 1992, Montevecchi and Myers 1996, Oro and Pradel 2000). For example, expansion of Atlantic Puffin *Fratercula arctica* and Northern Fulmar *Fulmarus glacialis* colonies can only be explained by high immigration rates from larger, neighboring colonies (Harris 1983, Stenhouse and Montevecchi 1999, Burg et al. 2003). Genetic techniques have also provided support for high rates of dispersal in seabirds. Birt-Friesen et al. (1992) found that despite evidence of philopatry from resighting studies, there is little genetic differentiation between North Atlantic colonies of Thick-billed Murres *Uria lomvia* suggesting that extensive dispersal has likely occurred in the recent past. Nevertheless,

there is still relatively little direct evidence (i.e., from individually marked birds) to provide quantitative assessments of seabird dispersal.

Dispersal of birds can occur both by established breeders changing breeding sites (breeding dispersal) or by birds nesting away from their natal breeding area (natal dispersal, Greenwood and Harvey 1982). The rate of breeding dispersal is low for most alcids ranging from 22% in the Ancient Murrelet *Synthliboramphus antiquus* (Gaston 1992) to only 4% in the Common Murre *Uria aalge* (Birkhead 1977). Breeding dispersal is often associated with a number of proximate factors including the presence of predators (Alonso et al. 1997, Bried and Jouventin 1999, Cam et al. 2004), environmental events such as flooding (Veit and Prince 1997, Schjorring 2001), and failed breeding attempts (Gaston 1992, Cam et al. 2004). Dispersal also occurs naturally in a population, independent of disturbance events. Irrespective of the cause, dispersal forms an essential component of metapopulation and source-sink dynamics, aiding in recolonization and maintaining gene flow (Paradis et al 1998, Oro and Ruxton 2001, Breton et al. 2006).

The Razorbill *Alca torda* is the least numerous alcid breeding in Atlantic Canada with an estimated total breeding population of less than 38,000 breeding pairs (Chapdelaine et al. 2001). Most colonies are located from north-central Labrador to the Gulf of Maine and west into the Gulf of St. Lawrence (Hipfner and Chapdelaine 2002). Most colonies are small ranging from a few hundred to a thousand breeding pairs (Chapdelaine et al. 2001), and like many seabirds, the movement of individuals among colonies has been poorly studied. Here we present the results of a long-term study examining the dispersal behavior of the Razorbill in Atlantic Canada in relation to population change. In summary, the objectives of our study were to quantify

Razorbill dispersal rates from two sites near the northern and southern limits of the species' range in Canada, and to evaluate the implications of dispersal rates for population monitoring methodology and Razorbill conservation.

## 3.1. METHODS

### *3.1.1. Study sites*

The primary field study sites for this project were the Gannet Islands, Labrador, Canada (53°56'N, 56°30'W) and Machias Seal Island, New Brunswick, Canada (MSI; 44°3'N, 67°06'W). The Gannet Islands cluster includes six islands (GC1-GC6) ranging in size from 4 to 125 hectares. The Gannet Islands are located 50 km southeast of Groswater Bay and are home to the largest Razorbill breeding colony in Atlantic Canada (Figure 3.1) with an estimated 9,800 breeding pairs (Chapdelaine et al. 2001). MSI is a four hectare island located in the Bay of Fundy and is home to approximately 543 Razorbill pairs (Grecian 2005). Additional field work was conducted on the Herring Islands, Labrador, Canada (54°20'N, 57°7'W), Petit Manan Island (PMI), Seal Island (SI), and Matinicus Rock (MR), Maine, United States (approximately 44°23'N, 67°49'W).

We also had access to data on Razorbill chicks and adults banded in Quebec from 1986-2006 by Canadian Wildlife Service (CWS) personnel as part of a long-term monitoring program. Banding effort was concentrated primarily on île Sainte-Marie and île aux Perroquets located along the north shore of the Gulf of St. Lawrence (50°3'N, 59°6'W, approximately 7,300 breeding pairs, Chapdelaine et al. 2001).

### 3.1.2. *Banding and resighting*

Razorbills were banded with size five CWS triangular stainless steel leg bands. Collectively more than 12,000 Razorbills have been banded (most as chicks) in eastern Canada from 1986-2006 (Table 3.1). Razorbill resighting effort was conducted regularly on the Gannet Islands and MSI from 2003 to 2006. In July 2005, we visited the Herring Islands, located 70 km north-west of the Gannet Islands in order to look for Razorbills which were banded on the Gannet Islands and are now breeding on the Herring Islands. Resighting data for Razorbills on PMI, Seal Island, and Matinicus Rock were provided by U.S. Fish and Wildlife Service and National Audubon Society personnel. Razorbills resighted at a location other than where they were banded were entered into a database. For all birds we attempted to confirm breeding status through observations of copulation, incubation of an egg or chick, chick-provisioning event, or presence of a brood patch. An individual bird was not considered to be confirmed or entered into the database until it had been resighted at least twice from 2003-2006, to account for the possibility of band reading error (see Chapter 2). This would likely reduce the chance of error to less than 0.001% (i.e., 0.035 x 0.035; Chapter 2), but unavoidably cause the omission of the individuals that were correctly resighted only once. For this reason our estimates of dispersal were likely minimum estimates.

### 3.1.3. *Philopatry and breeding dispersal*

Monitoring of individual breeding adults and their respective breeding sites has proven challenging in Razorbills because most birds nest in inaccessible crevices and under boulders (Rowe and Jones 2000, Hipfner and Chapdelaine 2002). To determine the nesting location of individuals, researchers often need to enter the colony and capture each bird on its nest.

Razorbills on the Gannet Islands are highly sensitive to disturbance and will often abandon their nest if disturbed by people (Hipfner and Bryant 1999). As a result, for most marked individuals we were only able to determine if a breeding adult had returned to the same colony (not breeding site) each year. We refer to a breeding colony as a group of occupied nest sites or crevices separated by at least 100 m of unoccupied habitat from other nest sites. Therefore a bird was considered to have changed its colony if its nest site was at least 100 m from its natal site (Figure 3.1). All birds that moved between islands in the Gannet Island archipelago were considered to have changed colonies.

We were not able to use multi-state capture-mark-recapture (CMR) models to calculate dispersal rates between the Gannet Islands, MSI, and Quebec and within islands in the Gannet Islands cluster due to uneven resighting effort across islands and years and the low number of birds involved in long-distance dispersal events. Philopatry and colony fidelity rates were determined for the Gannet Islands based on more than 3300 resightings of individually marked birds during 1996-2006. A position fix for each sighting was recorded using GPS and we calculated the distance that individual birds dispersed between banding as a chick and return as an adult, and for adults between breeding seasons. To calculate dispersal rates between colonies and islands within the Gannet Islands cluster and to account for mortality of birds, we determined whether birds were: (a) resighted at the same colony where banded ($N_p$ = number philopatric), (b) resighted at a different colony site on the same island where banded ($N_c$ = number that changed colony), or (c) resighted on a different island within the Gannet Islands cluster (($N_i$ = number that changed island). Dispersal rates between islands were calculated using the following formula: $N_i/(N_p+N_c+N_i)$.

## 4.1. RESULTS

### *4.1.1. Long-distance dispersal events*

Forty Razorbills (37 banded as chicks and 3 banded as adults) that were banded in one colony and later resighted at a different colony during 1971-2006 (Table 3.2). Ten birds dispersed to the Gannet Islands from across eastern Canada. One bird (band number 785-41398) banded as a chick on Digges Island (62°34'N, 77°42'W), Nunavut in 1982, was later resighted and recaptured on the Gannet Islands in 2003-2006. Another bird (band number M-16909), banded as a chick on Handa Island, Scotland (58° 23' N, 5°11' W) in 1971 was seen four times on the Gannet Islands in 2004, more than 3200 kilometers away. Fifteen of the birds that were resighted were three years of age or younger, so likely were not breeding (Lloyd and Perrins 1997). However, breeding status was confirmed for seven birds including the bird banded in Nunavut and two from Quebec.

### *4.1.2. Philopatry and breeding dispersal*

Of 314 birds banded as a chick on the Gannet Islands, 260 (83%) were observed breeding on their natal island (Table 3.3). Of these, 214 (82%) returned to within 100 m of their natal colony. Fidelity was higher for birds banded as adults (n = 149) with 97% of birds returning to the same breeding colony. Mean distance moved (in meters) between breeding sites on the same island was 241±29SE (n = 43) for birds banded as chicks and 317±128SE (n = 4) for adults. Mean distance moved between different islands (within the Gannet Islands cluster) for birds banded as chicks and adults was 541±34SE (n = 41) and 783±198SE (n = 4), respectively. Dispersal rates for each island (GC1-GC5) in the cluster varied greatly with GC3 and GC5 exhibiting the highest emigration rates (100%; Table 3.3).

## 5.1. DISCUSSION

Emigration of immature birds can greatly influence estimates of local survival to breeding age (Harris 1983, Cilimburg et al. 2002, Marshall et al. 2004). Therefore it is necessary to quantify emigration and immigration rates before detailed life tables for the species are constructed. The main difficulty with this is that observers tend to concentrate their search efforts at the colonies where birds were banded. Ideally, neighboring colonies should be visited regularly or at least until no new sightings or recoveries are recorded. Furthermore, seabird breeding colonies are sometimes regarded as independent entities in population surveys, neglecting the possibility that declines at one colony could reflect dispersal to alternate sites. In order to clarify the rate and role of dispersal in Razorbill population dynamics, we collated and interpreted resighting records from five locations that extend over almost the entire North American breeding range of Razorbills.

Numerous records of long-distance movements in Razorbill exist, ranging from 250 to 4130 kilometers (Lloyd 1974, Mead 1974, Bakken et al. 2003, Lyngs 2003). However, all of these records involve birds that were shot or found dead during the winter (i.e., the result of seasonal migration). Therefore, to our knowledge, our study provides the first record of long-distance dispersal of Razorbills to a new breeding colony as well as the first trans-Atlantic dispersal event for this species.

Prior to 2004, no Razorbills were known to breed on PMI or SI (L. Welch and S. Hall, pers. comm.). The recent colonization of these islands by Razorbills appears to be at least partially the

result of dispersal of individuals from nearby MSI. In 2006 alone, 15 banded Razorbill were resighted on PMI, SI, and MR (one bird, age 3, has been confirmed as a breeder on PMI).

Census data for Razorbills breeding on the Gannet Islands over the past 28 years suggest that the local population is increasing (Robertson and Elliot 2002). However, recent survival and productivity parameter estimates do not support this trend (i.e., estimates are too low to explain a stable or increasing population without immigration; Chapters 4 and 5, Lavers, unpublished data). The role of dispersal in maintaining populations is widely accepted and may thus explain the observed local population increases observed on the Gannet Islands. Eleven banded individuals from across eastern Canada and one from Scotland were observed on the Gannet Islands over the course of this study. These individuals likely represent only a small proportion of the birds recruiting to the Gannet Islands because the appearance of new, un-banded individuals can not be detected. This pattern has also been reported for Razorbills on Graesholmen, Denmark where birds from foreign colonies may account for up to 50% of annual population increase (Hipfner and Chapdelaine 2002). At the Gannet Islands during 1996-2006, researchers inadvertently afforded protection to the Razorbill breeding colonies there by deterring human predation (hunting, egging and associated disturbance) and removing Arctic foxes (*Alopex lagopus*) that regularly invade, thus creating conditions that may be attractive to immigrants. While the local population increase at the Gannet Islands may be taken as possible 'good news' for a species considered to be depleted by centuries of hunting and egging and by possibly by recent fisheries bycatch and oil pollution, the reported increase would have low overall population significance if it was due mainly to immigration from other more disturbed colony sites.

Philopatry rates for Razorbills banded as chicks on the Gannet Islands were high with 87% of individuals returning to breed on their natal island and 66% returning to their natal colony. These findings are comparable to those for closely related species such as the Common Murre *Uria aalge* and Atlantic Puffin *Fratercula arctica* (Harris et al. 1996, Breton et al. 2006a), but were significantly lower than reported for Razorbills on Skokholm, Wales (philopatry = 99.5%, Lloyd 1974). Overall, philopatry and therefore dispersal rates within the Gannet Islands cluster varied greatly depending on the island, with frequently disturbed islands exhibiting the highest rates of emigration. Individuals banded on islands GC3 and GC5 exhibited the lowest rates of philopatry with 80% and 100% of individuals dispersing to breed on another island, respectively. Although GC5 suffers from small sample size, the behavior of these few birds is likely representative of the island population as a whole. In seabirds, high levels of disturbance and breeding failures have been shown to cause divorce of established pairs and encourage dispersal to new and potentially more productive sites (Greenwood and Harvey 1982, Choudhury 1995). Compared to other islands in the cluster, GC5 is the most frequently invaded by Arctic foxes *Alopex lagopus* which in the past, resulted in the complete abandonment of all colonies on the island (Robertson and Elliot 2002, Lavers unpublished data). Similar issues exist for GC1 and GC3 with both islands suffering from gull predation (Lavers pers. obs). In addition, the main Razorbill colony on GC3, located on a low-lying beach, is affected by occasional flooding during high seas resulting in chick mortality. Emigration from Machias Seal Island to other (until recently unoccupied) islands in the Gulf of Maine can be explained by high population density at the tiny MSI (population rapidly expanding), providing emigrants to nearby small islands with abundant breeding sites available.

Current survival estimates for Razorbills on the Gannet Islands and MSI (see Chapter 4) have been quantified with the inclusion of resighting records for birds which dispersed to other colonies. These estimates are lower than other estimates for this species and do not predict a stable population without immigration. For seabird population managers, our results indicate the need for complete surveys of all colonies in the region, to ascertain whether the overall population is stable, increasing, or decreasing and the relative roles of different anthropogenic factors in Razorbill population dynamics.

ACKNOWLEDGMENTS

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Figure 3.1. Map of eastern Canada showing some of the locations where Razorbills have been banded and resighted.

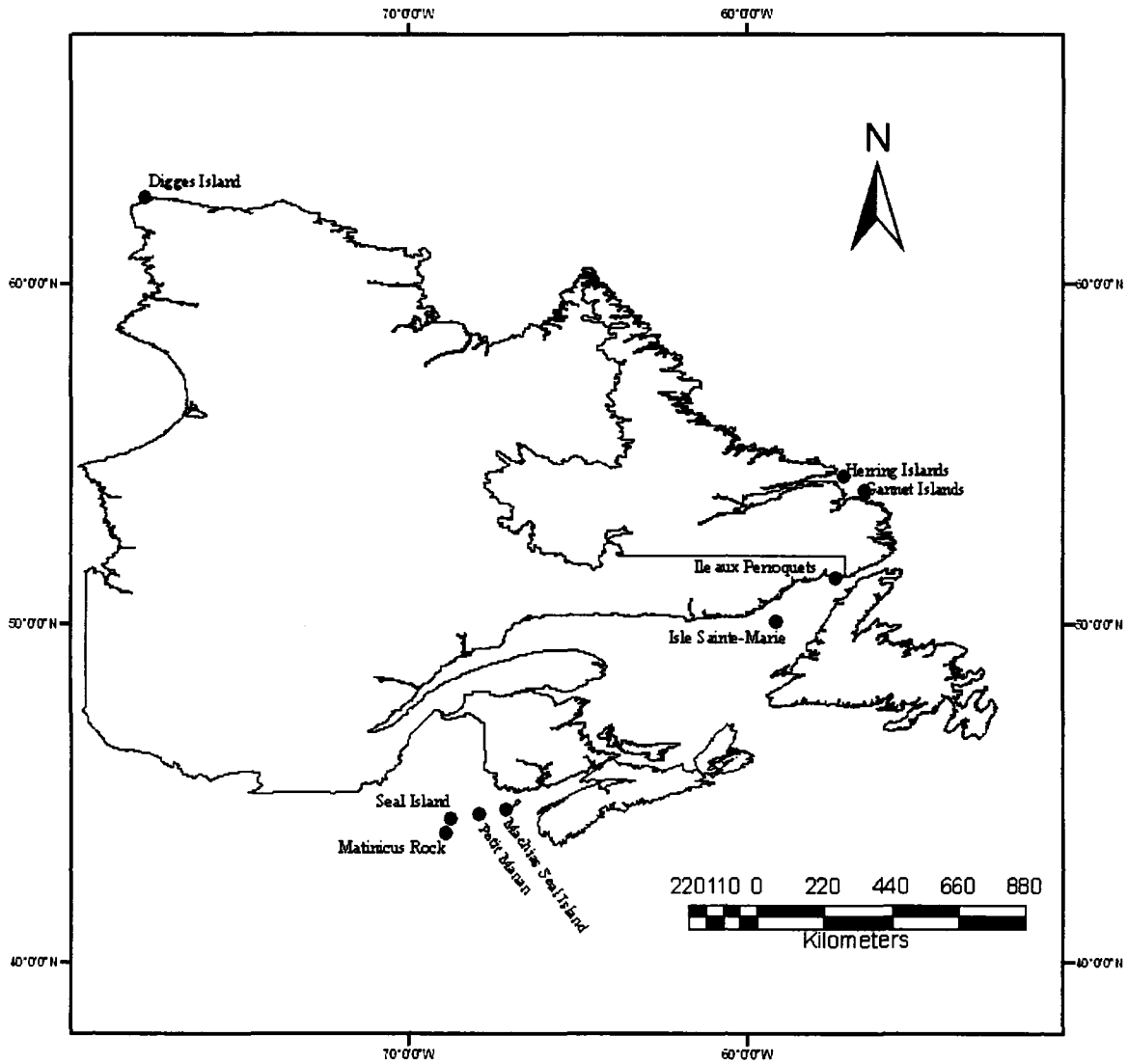

Table 3.1. Summary of re-sightings of Razorbills at sites in Eastern Canada where >1000 birds had been banded.

| Location and year of banding | No. of birds banded | | No. of birds resighted at the Gannet Islands and Machias Seal Island | |
|---|---|---|---|---|
| | Chicks | Adults | Banded as chicks | Banded as adults |
| Gannet Islands 1996-2006 | 5,575 | 350 | 330 | 160 |
| Machias Seal Island 1995-2006 | 722 | 327 | 176 | 161 |
| île Sainte-Marie 1986-2006 | 2,990 | 877 | 2 | 0 |
| île aux Perroquets 1986-2006 | 1,144 | 279 | 1 | 1 |

Table 3.2. Summary of the inter-island long-distance movements of Razorbills recorded from 1971 to 2006.

| Banding Location | Resighting Location | Number of Individuals | | Distance (km) |
|---|---|---|---|---|
| | | Banded as Chicks | Banded as Adults | |
| Gannet Islands | Herring Islands | 5 | 0 | 57 |
| | Machias Seal Island | 2 | 1 | 1298 |
| Herring Islands | Gannet Islands | 4 | 0 | 57 |
| Machias Seal Island | Gannet Islands | 1 | 1 | 1298 |
| | Petit Manan | 10 | 0 | 136 |
| | Seal Island | 3 | 0 | 195 |
| | Matinicus Rock | 7 | 0 | 161 |
| Digges Island | Gannet Islands | 1 | 0 | 1737 |
| Quebec | Gannet Islands | 3 | 1 | 474 |
| Handa Island | Gannet Islands | 1 | 0 | 3210 |

Appendix 3.1. Raw data for all Razorbills resighted during this study at a location other than where they were banded. Exact dates given when available (waiting on update from L. Welch, USFWS)

| Band No. | Date banded | Loc banded | Age | Dates resighted | Site resighted | Distance (km) | Breeding? |
|---|---|---|---|---|---|---|---|
| 895-13522 | 22-Jul-97 | Gannet Island | AHY | 4-Jun-05 | Machias Seal Is. | 1298 | Yes |
| 895-13866 | 3-Aug-99 | Gannet Island | L | 24-May-04 | Machias Seal Is. | 1298 | |
| 895-13978 | 29-Aug-97 | Gannet Island | L | 23-May-04 | Machias Seal Is. | 1298 | |
| 895-16480 | 14-Aug-02 | Gannet Island | L | 25-Jul-05 | Herring Islands | 57 | |
| 895-16709 | 6-Aug-01 | Gannet Island | L | 25-Jul-05 | Herring Islands | 57 | |
| 895-16798 | 6-Aug-01 | Gannet Island | L | 23-Jul-05 | Herring Islands | 57 | Yes |
| 895-17880 | 14-Aug-03 | Gannet Island | L | 23-Jul-05 | Herring Islands | 57 | |
| 895-18363 | 23-Aug-98 | Gannet Island | L | 26-Jul-05 | Herring Islands | 57 | Yes |
| 895-19528 | 23-Jul-05 | Herring Islands | L | 9-Jul-06 | Gannet Islands | 57 | |
| 895-19542 | 23-Jul-05 | Herring Islands | L | 8-Jul-06 | Gannet Islands | 57 | |
| 895-19544 | 23-Jul-05 | Herring Islands | L | 6-Aug-06 | Gannet Islands | 57 | |
| 895-19584 | 23-Jul-05 | Herring Islands | L | 8-Jul-06 | Gannet Islands | 57 | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 895-13587 | 18-May-00 | Machias Seal Island | AHY | Jul 16 & 18/03 | Gannet Islands | 1298 | |
| 895-14073 | 28-Jun-00 | Machias Seal Island | L | Jul 11 & 18, 2006 | Gannet Islands | 1298 | |
| 895-14220 | 26-May-01 | Machias Seal Island | L | 19-Jun-06 | Matinicus Rock | 161 | |
| 895-14290 | 23-Jun-01 | Machias Seal Island | L | 28-Jun-2004 | Petit Manan | 136 | |
| 895-17022 | 29-Jun-01 | Machias Seal Island | L | 22-Jun-06 | Matinicus Rock | 161 | |
| 895-17058 | 17-Jul-01 | Machias Seal Island | L | 28-Jun-2004 | Petit Manan | 136 | Yes |
| 895-17082 | 15-Jul-01 | Machias Seal Island | L | 2005 | Seal Island | 195 | |
| 895-17099 | 29-Jun-01 | Machias Seal Island | L | 22-Jun-06 | Matinicus Rock | 161 | |
| 895-17102 | 1-Jul-01 | Machias Seal Island | L | 16-Jul-2004 | Petit Manan | 136 | |
| 895-17141 | 18-Jul-01 | Machias Seal Island | L | Jul 2, 8 & 15, 2006 | Petit Manan | 136 | |
| 895-17146 | 20-Jul-01 | Machias Seal Island | L | 19-Jun-06 | Matinicus Rock | 161 | |
| 895-17214 | 11-Jul-02 | Machias Seal Island | L | 2004 | Petit Manan | 136 | |
| 895-17216 | 11-Jul-02 | Machias Seal Island | L | May 28 & Jul 2, 2006 | Petit Manan | 136 | |
| 895-17236 | 11-Jul-02 | Machias Seal Island | L | 2-Jul-06 | Petit Manan | 136 | |
| 895-17243 | 11-Jul-02 | Machias Seal Island | L | 2005 | Seal Island | 195 | |
| 895-17278 | 6-Jul-03 | Machias Seal Island | L | 19-Jun-06 | Matinicus Rock | 161 | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 895-17280 | 6-Jul-03 | Machias Seal | L | 2006 | Matinicus Rock | 161 | |
| 895-17280 | 6-Jul-03 | Machias Seal Island | L | 14-Jun-06 | Seal Island | 195 | |
| 895-17291 | 9-Jul-03 | Machias Seal Island | L | 27-May-06 | Petit Manan | 136 | |
| 895-17325 | 6-Jul-04 | Machias Seal Island | L | 27-May-06 | Petit Manan | 136 | |
| 895-17347 | 14-Jul-04 | Machias Seal Island | L | 19-Jun-06 | Matinicus Rock | 161 | |
| 895-17407 | 22-Jul-04 | Machias Seal Island | L | 16-Jun-06 | Petit Manan | 136 | |
| 785-41398 | 1982 | Digges Island | L | 2003 to 2006 | Gannet Islands | 1554 | Yes |
| 895-14714 | 28-Jul-01 | île aux Perroquet | L | Jul 24 & Aug 13/03 | Gannet Islands | 463 | |
| 895-14729 | 28-Jul-01 | île aux Perroquet | AHY | 10-Aug-06 | Gannet Islands | 463 | |
| 996-04658 | 24-Jul-93 | île Sainte Marie | L | Jul 6 & Aug 13/04 | Gannet Islands | 474 | Yes |
| 996-04714 | 23-Jul-93 | île Sainte Marie | L | Jul 5, 19 & Aug 13/04 | Gannet Islands | 474 | Yes |
| M-16909 | 8-Jul-73 | Handa Island | L | 11-Jul-04 | Gannet Islands | 3210 | |

Table 3.3. Movements of Razorbills between islands within the Gannet Islands, Labrador cluster.

| Island | Number Banded | | Number resighted | | Number breeding at different colonal | | Number breeding on different island | | Dispersal Rate | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Chicks | Adults | Chicks | Adults | Chicks | Adults | Chicks | Adults | Chicks | Adults |
| GC1 | 1,423 | 1 | 43 | 0 | 3 | 0 | 16 | 0 | 0.37 | N/A |
| GC2 | 1,474 | 233 | 143 | 120 | 33 | 4 | 0 | 3 | 0.00 | 0.03 |
| GC3 | 1,084 | 31 | 20 | 0 | 1 | 0 | 20 | 0 | 1.00 | N/A |
| GC4 | 1,299 | 80 | 104 | 29 | 9 | 0 | 14 | 1 | 0.13 | 0.03 |
| GC5 | 190 | 1 | 4 | 0 | 0 | 0 | 4 | 0 | 1.00 | N/A |

[1]Breeding at a different colony on the same island bird was banded on.

# CHAPTER FOUR

# ANNUAL SURVIVAL OF ATLANTIC CANADIAN RAZORBILLS (*ALCA TORDA*) VARIES WITH CLIMATE AND OCEANOGRAPHY

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## 1.1. ABSTRACT

In long-lived seabirds, reproductive performance is the demographic trait that is assumed to be most affected by changing environmental conditions. There is much less evidence that survival, especially of breeding adults, is dependent on environmental conditions. However, recent studies of a number of seabirds have found that ocean climate indices such as the Pacific Decadal Oscillation Index and sea surface temperature are correlated with adult survival. Here we evaluated whether annual adult survival of Razorbills *Alca torda* at two breeding colonies covaried with oceanographic conditions in the North Atlantic during 1995-2006. We also examined pre-breeder survival (from fledging to age 2). The relationships between local adult survival and the North Atlantic Oscillation and two oceanographic variables (Labrador Current temperature profile and Bay of Fundy sea surface temperature) were evaluated using program MARK. Capture-mark-recapture data fit the assumptions of program MARK reasonably well with ĉ values ranging from 1.390 to 2.404. Pre-breeder survival rates were high for MSI ($\Phi$ = 0.778 ± 0.041) and low for the Gannet Islands ($\Phi$ = 0.482± 0.033), likely the result of hunting pressure. On Machias Seal Island, constant survival ($\Phi$ = 0.967± 0.028) was the best model; however time-dependent models that included a climate covariate performed nearly as well. On the Gannet Islands, adult survival ($\Phi$ = 0.890± 0.053) was negatively correlated with the Labrador Current temperature profile. Our results show significant differences in survival rates across sites over the same time period and highlight the importance of multi-site studies and small-scale climate indices for local populations.

## 2.1. INTRODUCTION

According to life-history theory, in most long-lived seabirds, adult survival has the highest elasticity, meaning that this parameter explains the most variation in lifetime reproductive success (Croxall and Rothery 1991, Sandvik et al. 2005). Adult survival has therefore been assumed to be the life-history trait that would be least affected by climate variability (Cairns 1987, Gaillard and Yoccoz 2003). Early studies focused on seabird productivity and diet as being the most sensitive to changing environmental conditions (Nettleship and Birkhead 1985, Montevecchi 1993). More recently, extreme weather conditions such as El Niño Southern Oscillation events (ENSO; Barber and Chavez 1983), storms (Underwood and Stowe 1984, Harris and Wanless 1996) and hurricanes (Morris and Chardine 1995) have been shown to be linked to direct and indirect adult mortality. Growing evidence now implicates seabird annual adult survival as being linked to continuous variation in climate (Thompson and Ollason 2001, Weimerskirch et al. 2001, Jones et al. 2002, Durant et al. 2004, Grosbois and Thompson 2005, Jones et al. *in press*) with similar broad trends for many aspects of marine ecosystems (i.e., prey availability; Aebischer et al. 1990, Nakashima 1996, Alheit and Hagen 1997, Hjermann et al. 2004). The urgent questions are now how widespread are these reported tendencies across seabird species and populations, and what are the mechanisms that explain patterns of covariation between survival and environmental conditions?

Ocean climate varies considerably between years and has been characterized by indices such as the North Pacific Index, Pacific Decadal Oscillation, and ENSO (Trenberth and Hurrell 1994, Zhang et al. 1997). In the North Atlantic, the most pronounced index is the North Atlantic Oscillation (NAO), which is derived as the pressure differential between the subtropic high-

pressure zone centered over the Azores and the atmospheric low-pressure zone over Iceland (Ottersen et al. 2001, Hurrell et al. 2003). The NAO exerts a dominant influence on winter sea surface temperature (SST). When the NAO index is positive, strong northerly winds over Greenland and Canada carry cold wind southward resulting in decreased SST over the northwest Atlantic (Hurrell and Dickson 2004). Since the 1980s, the NAO has been in a mostly positive phase, resulting in colder and stormier winters (Hurrell and Dickson 2004). Such changes in surface temperature (and related changes in rainfall and storm frequency) can have significant impacts on marine organisms, including seabirds. Here we examine the relationship between climate covariates such as the NAO and adult survival in a long-lived seabird, the Razorbill *Alca torda* over a twelve year period at two breeding colonies which extend over almost their entire North American breeding range. The aims of our study were: (1) to quantify annual adult and pre-breeder (from fledging to age two) survival of Razorbills at two representative colony sites in the western Atlantic during 1995-2006, (2) to examine whether adult survival covaried with climate indices, and (3) evaluate possible mechanisms for any patterns observed.

## 3.1. METHODS

### *3.1.1. Study sites*

Fieldwork was conducted at the Gannet Islands, Labrador, Canada (53°56'N, 56°30'W, Figure 4.1) and Machias Seal Island, New Brunswick, Canada (MSI, 44°3'N, 67°06'W). The Gannet Islands cluster includes six islands (GC1-GC6) which support the largest colony of Razorbills in North America (c. 9,800 breeding pairs; Chapdelaine et al. 2001). The Gannet Islands represent one of the most northerly major Razorbill breeding colonies in North America. In contrast, MSI

is located at the southern extent of the Razorbills breeding range and supports 543 pairs (Grecian 2005).

*3.1.2. Capture-mark-recapture/resight*

Adult Razorbills were captured from June to early August from 1995-2006 using noose carpets attached to prominent display rocks (adjacent to the breeding sites) where birds gathered daily to socialize. Razorbill chicks were captured by hand or with a small net when they were about 10 days of age. This was the preferred age for banding since the chicks were able to thermoregulate, but had limited mobility and could be captured on steep cliffs with minimal disturbance. Adults and chicks were banded with size five U.S. Fish and Wildlife Service triangular stainless steel leg bands. Banding of Razorbills on MSI and the Gannet Islands began in 1995 and 1996, respectively, and since then, 7,039 birds (mostly chicks) have been banded. Nine bands were replaced on MSI and two on the Gannet Islands during this study due to wear and erosion of the bands caused by the birds walking over rough terrain (Lyngs 2006).

Razorbill resighting effort was conducted on the Gannet Islands and MSI from 1995 to 2006. In July 2005, we also visited the Herring Islands (54°20'N, 57°7'W), located 70 km north-west of the Gannet Islands in order to look for Razorbills originally banded on the Gannet Islands that are now breeding on the Herring Islands. We also sought evidence for Razorbill dispersal from MSI. Resighting data for Razorbills on Petit Manan Island (44° 23'N, 67° 49'W), Seal Island, and Matinicus Rock (approximately 44°23'N, 67°49'W) in the Gulf of Maine were provided by U.S. Fish and Wildlife Service and National Audubon Society personnel. An individual bird was not considered confirmed or entered into the database until it had been resighted at least twice

from 1995-2006. This would likely reduce the chance of band reading errors (see Chapter 2), but unavoidably cause the omission of individuals that were correctly resighted only once. On the Gannet Islands, 101 birds banded as chicks and 13 adults were seen only once over the study period. On MSI, 34 birds banded as chicks and 22 adults were also only seen one time. These birds were excluded from the data set.

Banding and resighting effort varied greatly from 1995-1998 at both study locations, therefore some data collected during these years were excluded from the analyses. For example, on MSI only 15 adults were banded and four resightings recorded from 1995-1998. The removal of this small amount of data resulted in improved fit of the models and more accurate parameter estimates. On the Gannet Islands, adult resighting was initiated on one plot only in 1998. No birds banded as chicks were observed that year; therefore the pre-breeder survival data set begins in 1999.

*3.1.3. Environmental covariates*

To test the hypothesis that Razorbill annual survival covaried with oceanographic variability we looked for a correlation between survival and three North Atlantic climatic indices (Table 4.1): (1) NAO, (2) the Labrador Current (LC) as indicated by the ocean temperature profile (to 175 m depth) from Department of Fisheries and Oceans (DFO) Station 27 (Figure 4.1), and (3) sea-surface temperature (to 1 m depth) for the Bay of Fundy provided by DFO Station 5 (Figure 4.1). We used mean values from March of the previous year to March of the current year (i.e., the 12 months leading up to the start of the current breeding season; M-M $_{t-1}$) as well as the mean of the previous November to March (i.e., the 5 winter months leading up to the start of the current

breeding season; winter $_{t-1}$), mean of the current year (i.e., January to December of the current year), and the mean of November to March of the current year (i.e., the winter months immediately following the current breeding season; winter $_t$).

*3.1.4. Model selection*

Apparent survival ($\Phi$) and recapture probabilities ($p$) were estimated using capture-mark-recapture/resight (CMR) models (Lebreton et al. 1992) with program MARK (White and Burnham 1999). For birds banded as chicks, there was significant variation in recapture rate for all cohorts in all years at both study locations. Variability in resighting rate is known to create problems in estimating survival (Martin et al. 1995, Prévot-Juilliard et al. 1998), so we evaluated models with a different recapture rate parameter for each year and cohort until the birds reached adulthood at age three (i.e. complete time dependence; $p$(cohort)) and with recapture rate parameters that were pooled across similar years (i.e. $p$(pooled)).

Since our marking technique was known to catch both non-breeding and breeding adult birds, we expected that some individuals ('prospectors') might show lower site fidelity, and hence lower local survival rates, after their first capture (Pradel et al. 1997, Prévot-Juilliard et al. 1998, Bertram et al. 2000). We allowed survival rates in the year after the initial capture to be modeled independently of survival in subsequent years. Structurally, this is similar to age models (Lebreton et al. 1992). In these models, apparent survival after first year of capture is a combined estimate of true survival and permanent emigration rates (because the sample of marked individuals includes transient birds), while survival in subsequent years (of resident individuals) is a better approximation of true survival (Pradel et al. 1997). In summary, for our

global model for adults, we used a two-age class survival model with time dependence in all years after initial capture and time dependence in recapture probability.

Since most juvenile Razorbills do not return to the colony to prospect or breed until at least two years of age (Lloyd and Perrins 1977) and are therefore not available to be resighted, it was not possible to estimate annual survival during their first year of life. Instead, we estimated survival from fledging to age two (a0-2), referred to as pre-breeder survival. These models were similar to models for adults such that apparent survival from first capture until age two was a combined estimate of true survival and permanent emigration.

The goodness-of-fit of the global model to the data was determined using the parametric bootstrap approach described in Cooch and White (2001). From these bootstraps, we extracted a mean of the model deviance and a mean $\hat{c}$. $\hat{c}$ is a measure of overdispersion, or extra-binominal variation, in the data. It arises when some model assumptions are not met, such as variation in survival or recapture rates among individual animals (Burnham and Anderson 1998). The observed deviance and $\hat{c}$ were divided by the mean of bootstrapped values, and the higher of the two values were taken as an estimate of $\hat{c}$ (Cooch and White 2001). We restricted our candidate models to the global model, plus a series of reduced parameter models to assess whether age-structure was appropriate. We did not construct every reduced parameter model, as this would have led to a large number of models, many of which had poor fit. Instead, we used the approach described in Lebreton et al. (1992) by first modeling recapture rates to determine the best structure and then modeling survival rates.

We modeled the climate covariate with survival only after the initial capture period, as we were not interested in the influence of oceanographic conditions on birds not resident in the study area. Model selection was based on comparison of the QAICc (Akaike Information Criterion), where the models with lowest QAICc values suggest the best compromise between good fitting models and models with relatively fewer explanatory variables (i.e., parsimonious; Anderson and Burnham 1998). QAICc, instead of AICc was used to rank models, as an acknowledgment of the extra-binomial variation in the data set, represented by ĉ (Burnham and Anderson 1998). QAICc weights were also calculated, as they provide a relative measure of how well a model supports the data compared with other models (Anderson and Burnham 1998). For all models we used notation similar to Lebreton et al. (1992), where the parameterization of each class was explicitly described (y1 = first year class, y2 = second year class, y3+ = all subsequent year classes) using t for time (year) effects. We used year classes instead of age classes since the age of birds banded as adults is not known.

## 4.1. RESULTS

### *4.1.1. Dispersal of Razorbills*

Survival rates were inferred from resightings of marked individuals. Because adult Razorbill breeding site fidelity is high (see Chapter 3 and Gaston and Jones 1998), there is likely little permanent emigration and our approach provides a close approximation to true survival. However, philopatry (birds banded as chicks) on the Gannet Islands was relatively low (see Chapter 3) and dispersal of individuals outside the study area was a concern. We attempted to account for this by including resightings of birds which had dispersed to other islands (i.e. these birds were marked as alive). Resighting was conducted on three islands in the Gulf of Maine and

on the Herring Islands in order to look for birds that dispersed from the island where they were banded. We found a total of five birds that dispersed from the Gannet Islands to the Herring Islands and 12 from MSI that dispersed to another island in the Gulf of Maine (all banded as chicks, see Chapter 3 for details). In addition, three birds banded on the Gannet Islands (one as an adult) were later resighted on MSI and one bird banded as an adult on MSI was resighted on the Gannet Islands. Only four of the dispersal birds were known to be breeding on their new island and it is possible that the remaining 17 birds are vagrants and may be attending both colonies (3 birds were seen on both the Gannet Islands and MSI and one bird was seen on Matinicus Rock and Seal Island). These birds were included in the CMR data set even though they had moved outside the main sampling area.

*4.1.2. Gannet Islands: adult survival*

A total of 311 Razorbill adults were captured on the Gannet Islands of which 191 were resighted at least twice. The data provided a good fit to our global model with two age classes. After constructing reduced parameter models, it was clear that recapture rate was best modeled without complete time dependence, but instead with seven time parameters that included three groups of years with similar recapture rates (very low: 1996 and 2001; moderate: 1999 and 2000; high: 1997 and 2002). Therefore only this parameterization (pooled) was used in building subsequent models. From the parametric bootstrap, $\hat{c}$ was calculated to be 1.390, suggesting the presence of some, but not major amounts of extra-binomial variation. This value of $\hat{c}$ was used to adjust all QAICc values. Models with two-age-structure were well-supported by the data (Table 4.2), and models with time dependent survival rates after initial capture (denoted y2+*t) were ranked

higher than models with constant survival. Therefore, we used survival rate after the first interval and recapture in three groups of years to model climatic covariates.

The most parsimonious model for birds banded as adults at the Gannet Islands in the candidate model set was a two-age class model in which survival covaried with the LC (station 27) climate index during the preceding March to March [$\Phi$(y1*t, y2+*Stn27 M-M $_{t-1}$) $p$(pooled); Table 4.2, Figure 4.2]. This model was four times better supported than the next best model (0.621/0.141 = 4.404). The slope β (based on a logit-linked analysis) of the relationship between survival and the LC was -5.04±0.85 SE (95% CI, -7.03 to -3.06; note the 95% confidence limits do not bound zero). It is possible to provide a mean survival rate after first capture for this model, however the estimate would be constrained by the covariate. Instead, we used the variance components method to take into account annual variance and sampling variance in survival rate (based on the model [$\Phi$(y1*t, y2+*t) $p$(pooled]). Our mean estimate of Razorbill adult survival at the Gannet Islands during 1996–2006 was 0.890 ±0.053 and recapture probability was 0.514±0.129.

*4.1.3. Gannet Islands: pre-breeder survival*

The banding and especially resighting data for birds banded as chicks on the Gannet Islands from 1996-1998 were quite sparse and inclusion of these data lead to many problems. Once these data were removed from the data set, the fit of the models improved significantly and the parameters could be estimated. A total of 885 chicks were banded on the Gannet Islands (island GC2 only) from 1999-2006, of which 157 were resighted at least twice. The data provided a reasonably good fit to our global model with two age classes and time dependence in survival rate and time variance in recapture rate. From the parametric bootstrap, ĉ was calculated to be 2.404

suggesting the presence of considerable extrabinomial variation. This value of ĉ was used to adjust all QAICc values.

After constructing reduced parameter models, it was clear that recapture rate was best modeled with years with similar probabilities pooled together. This parameterization was used is building subsequent models. The most parsimonious model for birds banded as chicks in the candidate model set was one with constant survival for ages 0-2 and 3+, and constant, pooled recapture probabilities for the first and second age classes followed by time dependence for the age 3+ class [$\Phi$ (y0-2, y3+) p(y1, y2, y3+*t); Table 4.3]. This model was more than two times better supported than the next best model (0.567/0.240 = 2.362). The mean estimate of Razorbill pre-breeder survival on the Gannet Islands 1996–2006 was 0.482±0.033 and was 0.921±0.03 once the birds were three years of age and older. Mean recapture probability was 0.113±0.039.

*4.1.4. Machias Seal Island: adult survival*

A total of 274 adult Razorbills were banded on Machias Seal Islands from 1999-2006 of which 193 were resighted at least twice. The data provided a reasonably good fit to our global model with two age classes and time dependence in survival rate and time dependence in recapture rate. From the parametric bootstrap, ĉ was calculated to be 1.671.

The most parsimonious model for birds banded as adults was a two-age class model with constant survival in the intervals following first capture and time dependence in recapture rate [$\Phi$(y1, y2+) $p$(t); Table 4.4]. This model was only slightly better supported than the next nine best models, all of which included a climate covariate (Table 4.4). Local adult Razorbill survival

on MSI in the year of banding is estimated at 0.752±0.054 and all subsequent years is 0.967±0.032 and recapture probability was 0.395±0.063.

*4.1.5. Machias Seal Island: pre-breeder survival*

The pre-breeder survival dataset (601 birds banded as chicks, 225 of which were later resighted at least twice) provided a reasonably good fit to the global model with two age classes and time dependence in survival rate and time dependence in recapture rates. From the parametric bootstrap, ĉ was calculated to be 1.492.

Machias Seal Islands pre-breeder model structure was very similar to the Gannet Islands with the most parsimonious model having two age classes and time independence for survival during the first two years following capture and pooled recapture probabilities for similar years [$\Phi$ (y0-2, y3+) $p$(y1*t, y2*t, y3+*t); Table 4.5). However, several models performed nearly as well (Table 4.4), their ΔAICc deviating by less than two from the optimal model. The survival estimates for the top model were 0.778 ± 0.041 for age class 0-2 years and 0.912 ± 0.052 for all subsequent years (3 years of age and older). Mean recapture probability was 0.176±0.056.

5.1. DISCUSSION

Our best-fitting models for local survival and recapture rate indicated that after initial capture some individuals (transients) permanently left the trapping area, and that adult survival at the Gannet Islands varied with the Labrador Current index. Local adult survival during the first interval after marking was 0.634± 0.038 for the Gannet Islands and 0.752± 0.054 for MSI, while survival thereafter averaged 0.890± 0.053 and 0.967± 0.028 respectively. These estimates

suggest that 21-25% of newly-marked adults were transients. Given the propensity for Razorbills to visit arena-like gathering areas (Wagner 1992), the capture of non-resident birds was not surprising. The survival estimates for birds age 3+ years from the known-age (i.e. banded as chicks) data set were higher on the Gannet Islands (0.971 ± 0.030) than the estimates generated using birds banded as adults, but were lower for MSI (0.912 ± 0.052; Table 6). We speculate that the slightly lower adult survival rate from birds banded as chicks on MSI may be due to the classification of possibly pre-breeding or inexperienced birds as adults. For example, birds age 3-5 are considered to be adults, but may not be breeding (Harris and Wanless 1989). If these young birds show slightly lower survival or site fidelity compared to the rest of the adult population, then lower survival rates are expected. Since the majority of chicks banded on MSI were banded between 1999 and 2006, most of the birds making up the known-age adult sample were 3-6 year olds. Band wear was detected on both study areas, with an indication that this was more prevalent at MSI, but this was not considered to be frequent enough to significantly modify the survival estimates.

Our adult survival estimates for Gannet Islands Razorbills fall within the lower range reported for Europe and Quebec (Lloyd 1974, Chapdelaine 1997, Poole et al. 1998, Harris and Wanless 1989, Sandvik et al. 2005; Table 6). However, among all studies, we found MSI to have the highest reported adult and pre-breeder survival rates (Table 6, Figure 2). This suggested there were differences in environmental conditions, mortality (e.g. hunting), or disturbance pressures such that the Gannet Islands population experienced lower true survival rates and/or higher rates of permanent immigration than MSI. However, there is little reason to suspect that the Gannet Islands would experience a higher rate of permanent immigration. Because breeding habitat is

not limiting on the Gannet Islands (Lavers 2007), there would appear to be no pressure for individuals to leave the area. At MSI, habitat is very limiting due to the small size of this single, isolated island so permanent emigration might be expected to be higher. Disturbance by researchers is controlled at both sites; however MSI, with 30-90 tourists permitted to visit the island per day during the summer (C. MacKinnon, personal communication, 2007), likely experiences higher disturbance overall. Taken together, these points suggest that if there was a difference in permanent emigration, it would have been higher at MSI (opposite to what is suggested by our local survival estimates).

Mortality would appear to be a better explanation for the difference in local survival rates between the Gannet Islands and MSI. Gannet Islands Razorbills are shot illegally during the annual Newfoundland murre hunt (Elliot 1991, Chapdelaine 1997), with 23 banded birds (one shot as an adult) occurring as recoveries since 1996 (Lavers 2007), suggesting that hunting alone could account for the lower survival rate. Ship and offshore oil and gas and gill nets off Newfoundland are two other sources of mortality that could affect the Gannet Islands population (Piatt and Nettleship 1987, Wiese 2002). Regardless of the cause, the survival difference has important population implications, especially for the Gannet Islands.

The best adult survival model for the Gannet Islands incorporated a climate covariate (Table 2), but MSI did not. This may be due partly to the shorter-term data set for MSI (1999-2006, 8 occasions) compared to the Gannet Islands (1996-2006, 11 occasions). Lack of correlation between climate and survival on MSI may also have been be due to the high adult survival estimate ($\Phi = 0.967$) which exhibited little inter-year variation. However, models incorporating

climate covariates performed nearly as well as the top model suggesting that with more years of data, it may be possible to detect a correlation between annual survival and climate at MSI.

In the north-eastern Atlantic, warm water currents such as the Slope and Norwegian Coastal Currents draw warm waters up from the south (McCartney and Talley 1982, Sherwin et al. 1999). Warm water is normally associated with reduced ocean productivity and poor feeding conditions for seabirds (e.g. Hatch 1987, Gjerdrum et al. 2003), so it was not surprising that in Norway, adult survival in three alcid species, including Razorbills, was found to be negatively correlated with Norwegian Sea SST and positively correlated with prey abundance (Sandvik et al. 2005). Our results suggest that adult Razorbill survival at the Gannet Islands was negatively correlated with Labrador Current temperatures, a dominant cold system in the north-west Atlantic. We speculate that adult Razorbills wintering in Newfoundland waters (like those from the Gannet Islands) have higher survival when the Labrador Current is cold due to increased primary productivity and recruitment of their prey that is the result of cooler conditions (Sundby 2000, Hirst and Kiorboe 2002). However, there likely exists a limit beyond which cold temperatures lead to reduced survival since, for the Labrador Current, it is anomalous cold years that cause poor growth and recruitment of marine organisms that seabirds prey on (Nakashima 1996, Dutil et al. 1999). None of these anomalous cold years occurred during the time-span of our study, but this phenomenon could have been important in the late 1980s and early 1990s immediately preceding our study (Montevecchi and Myers 1997).

Gannet Islands pre-breeder survival ($\Phi = 0.482$) was significantly lower than on MSI ($\Phi = 0.778$). This could have resulted either from higher rates of permanent emigration from the

Gannet Islands by pre-breeders, or from a greater mortality rate. Band recoveries of juvenile birds shot illegally are consistent with a role for the latter process (96% of Gannet Islands Razorbills shot in the hunt are pre-breeders; Lavers 2007). Unlike MSI Razorbills which winter primarily in the Gulf of Maine (Chapdelaine et al. 2001), Razorbills that bred on the Gannet Islands must migrate south through ice free waters south of Newfoundland (Brown 1985, Huettmann et al. 2005). The timing and migration route of Razorbills from Labrador overlap significantly with the timing and zones set out for the annual Newfoundland and Labrador murre (*Uria* spp.) hunt (Elliot 1991, Chapdelaine 1997). It is illegal to shoot Razorbills (except for Labrador Inuit, who are permitted to legally hunt Razorbills under the Migratory Birds Convention Act; Chardine et al. 1999), but due to their close physical resemblance to the murres, they are shot accidentally during the hunt. The number of Razorbills shot is not known, but recoveries of banded birds suggest that many hundreds to thousands may be shot each year (Elliot 1991, Chapdelaine 1997). Mortality from the hunt likely accounts for some (perhaps most) of the 27.8% difference in Razorbill pre-breeder mortality between the Gannet Islands population which is affected by the hunt, and the MSI population which is not.

By including observations of Razorbills on the Herring Islands and Gulf of Maine islands in the CMR data set, we attempted to partly account for the negative bias in the pre-breeder survival estimates that result from dispersal of birds outside the sampling area. However, resighting effort on the Gulf of Maine islands from 2004-2006 was significantly greater than at the Herring Islands, therefore dispersal from the Gannet Islands was likely underestimated.

A number of seabird studies have found that the NAO explains a larger portion of the variability in adult survival than smaller scale indices such as local SST (Grobois and Thompson 2005, Votier et al. 2005). Our data on survival and climatic suggest that regional climate conditions may explain a larger portion of the variation in adult Razorbill survival than large-scale climate indices like the NAO. This may be due in part to the Razorbills relatively limited and coastal range compared with other seabirds like the Northern Fulmar *Fulmarus glacialis* that are wide ranging and would be more likely to be influenced by large-scale climate (Frederiksen et al. 2004). Overall, these results underline the need for further long term detailed investigations into seabird demography and the influence of climate.

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Figure 4.1. Map of Atlantic Canada showing the Gannet Islands and Machias Seal Island in relation to Department of Fisheries and Oceans climate stations 5 and 27.

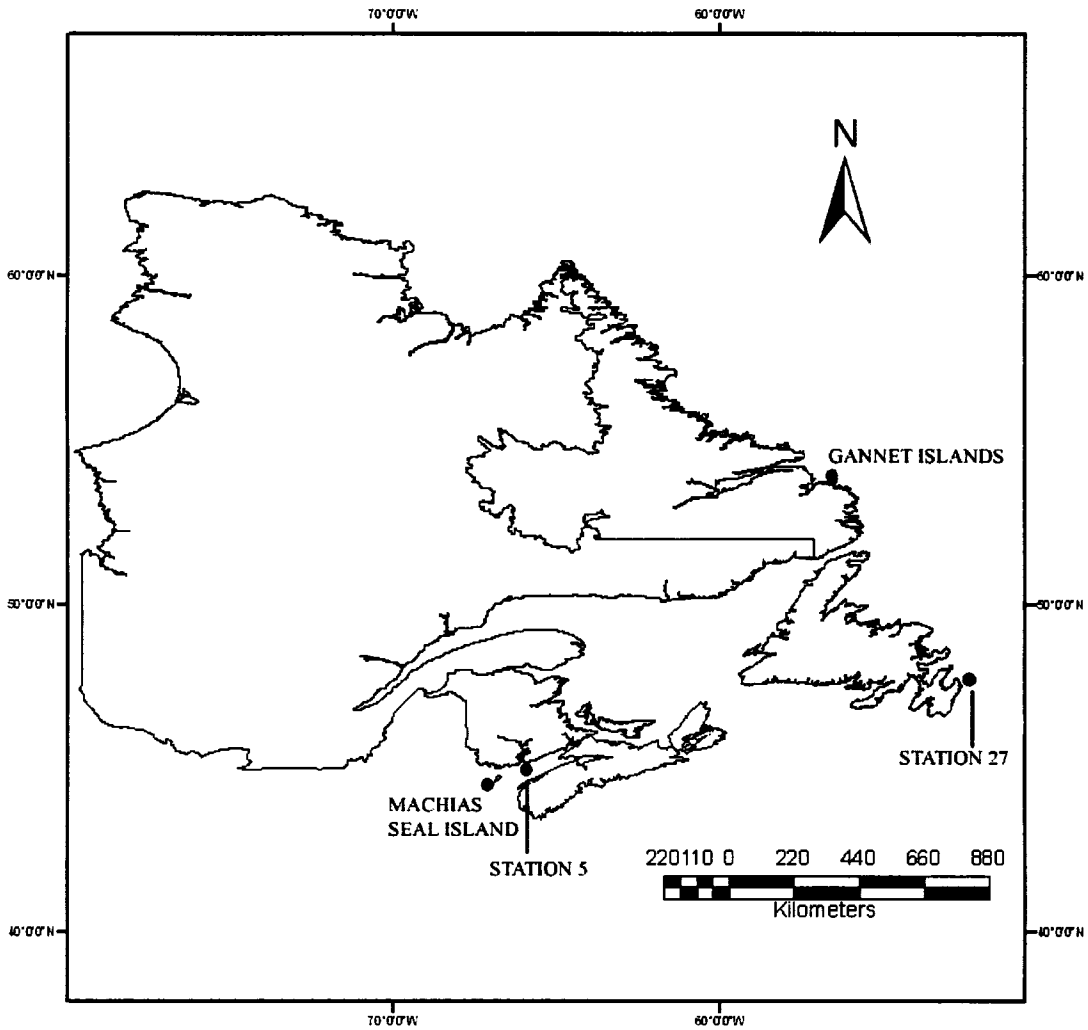

Table 4.1. Mean values of environmental covariates used in the analyses from March of the previous year to March of the current year.

| Year | North Atlantic Oscillation (NAO) | Station 27 (Labrador Current, °C) | Station 5 (Bay of Fundy, °C) |
|---|---|---|---|
| 1995 | 0.67 | 0.80 | 7.36 |
| 1996 | -0.27 | 0.85 | 6.56 |
| 1997 | 0.02 | 1.51 | 6.67 |
| 1998 | -0.15 | 0.94 | 6.67 |
| 1999 | -0.37 | 1.03 | 6.85 |
| 2000 | 0.52 | 1.35 | 7.43 |
| 2001 | -0.03 | 1.17 | 7.44 |
| 2002 | -0.05 | 1.27 | 6.97 |
| 2003 | 0.00 | 1.08 | 7.28 |
| 2004 | 0.08 | 1.43 | 6.39 |
| 2005 | 0.23 | 1.62 | 5.89 |

Table 4.2. Summary of the top 5 models tested for Razorbills banded as adults on GC2 and GC4 (Gannet Islands) from 1996-2006. Models are sorted by increasing QAICc (Akaike Information Criterion) value, with the most parsimonious model at the top. Subscripts reflect different factors in the model ($\Phi$ = survival parameter, y = year class (i.e. y1 = 1 year since banding), $p$ = resighting probability, pooled = years with similar recapture probability are pooled, t = time, M = March, #Par = number of estimable parameters, winter = November to March).

| Model ($\hat{c}$ = 1.390) | QAICc | ΔQAICc | Weight | Likelihood | #Par | QDev |
|---|---|---|---|---|---|---|
| $\Phi$(y1*t, y2+*Stn27 M-$M_{t-1}$) $p$(pooled) | 955.26 | 0.00 | 0.621 | 1.000 | 10 | 250.55 |
| $\Phi$(y1*t, y2+*Stn27 winter $_{t-1}$) $p$(pooled) | 958.22 | 2.96 | 0.141 | 0.228 | 10 | 253.51 |
| $\Phi$(y1*t, y2+*Stn5 M-$M_{t-1}$) $p$(pooled) | 959.23 | 3.97 | 0.085 | 0.137 | 10 | 254.52 |
| $\Phi$(y1*t, y2+*Stn5 winter $_{t-1}$) $p$(pooled) | 959.23 | 4.27 | 0.073 | 0.118 | 10 | 254.82 |
| $\Phi$(y1*t, y2+*Stn27$_t$) $p$(pooled) | 960.93 | 5.67 | 0.036 | 0.059 | 10 | 256.22 |

Figure 4.2. Adult Razorbill survival ($\Phi$) on the Gannet Islands, Labrador in relation to Station 27 Labrador Current sea temperature (°C) during 1998-2005.

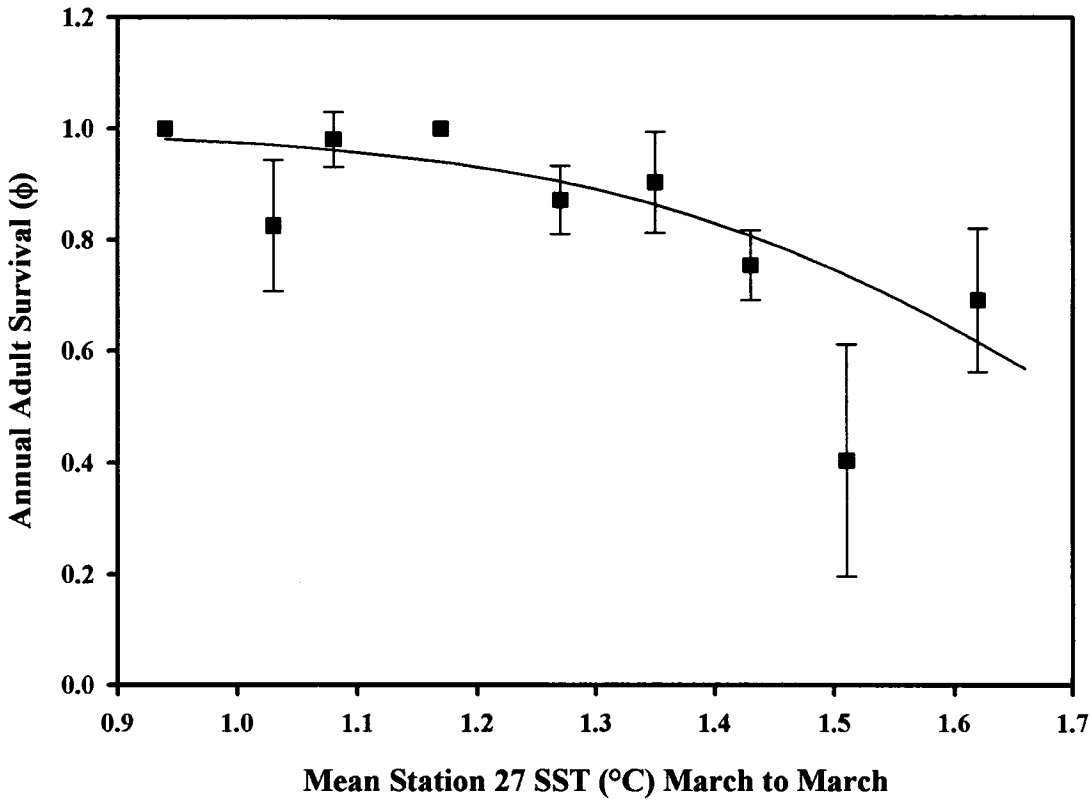

Table 4.3. Summary of the top 5 models for Razorbills banded as chicks on the Gannet Islands from 1999-2006. Models are sorted by increasing QAICc (Akaike Information Criterion) value, with the most parsimonious model at the top (see legend of Table 2 for explanation).

| Model ($\hat{c}$ = 2.404) | QAICc | ΔQAICc | Weight | Likelihood | # Par | QDev |
|---|---|---|---|---|---|---|
| $\Phi$(y0-2, y3+) $p$(y1,y2, y3+*t ) | 736.44 | 0.00 | 0.567 | 1.000 | 14 | 106.52 |
| $\Phi$(y0-2, y3, y4+) $p$(y0-2*t, y3+*t) | 738.17 | 1.72 | 0.240 | 0.423 | 15 | 106.19 |
| $\Phi$(y0-2, y3+) $p$(y1-3*t, y4+*t) | 738.60 | 2.16 | 0.192 | 0.340 | 15 | 106.63 |
| $\Phi$(y0-2, y3, y4+) $p$(y1-3*t, y4+*t ) | 748.86 | 12.41 | 0.001 | 0.002 | 16 | 114.82 |
| $\Phi$(y0-2, y3+) $p$(y0-2*t, y3+*t) | 764.99 | 28.55 | 0.000 | 0.000 | 29 | 103.92 |

Table 4.4. Summary of the top 5 models for Razorbills banded as adults on Machias Seal Island from 1999-2006. Models are sorted by increasing QAICc (Akaike Information Criterion) value, with the most parsimonious model at the top. Subscripts reflect different factors in the model (see legend of Table 2 for explanation).

| Model ($\hat{c}$ = 1.671) | QAICc | ΔQAICc | Weight | Likelihood | # Par | QDev |
|---|---|---|---|---|---|---|
| $\Phi$(y1, y2+) $p$(t) | 738.65 | 0.00 | 0.145 | 1.000 | 9 | 110.75 |
| $\Phi$(y1, y2+*Stn27 winter $_{t-1}$) $p$(t) | 739.49 | 0.84 | 0.095 | 0.657 | 10 | 109.50 |
| $\Phi$(y1, y2+*NAO winter $_{t}$) $p$(t) | 739.50 | 0.85 | 0.095 | 0.654 | 10 | 109.51 |
| $\Phi$(y1, y2+*Stn27 M-M $_{t-1}$) $p$(t) | 739.70 | 1.06 | 0.086 | 0.589 | 10 | 109.72 |
| $\Phi$(y1, y2+*Stn27 winter $_{t}$) $p$(t) | 739.79 | 1.14 | 0.082 | 0.566 | 10 | 109.80 |

Table 4.5. Summary of the top 5 models for Razorbills banded as chicks on Machias Seal Island from 1999-2006. Models are sorted by increasing QAICc (Akaike Information Criterion) value, with the most parsimonious model at the top (cohort = complete time and age dependence in recapture probability; see legend of Table 2 for explanation of other abbreviations).

| Model ($\hat{c}$ = 1.492) | QAICc | ΔQAICc | Weight | Likelihood | # Par | QDev |
|---|---|---|---|---|---|---|
| $\Phi$(y0-2, y3+) $p$(y1, y2, y3+*t) | 1085.94 | 0.00 | 0.296 | 1.000 | 20 | 72.52 |
| $\Phi$(y0-2, y3+) $p$(cohort) | 1087.17 | 1.23 | 0.160 | 0.541 | 30 | 52.37 |
| $\Phi$(y1, y2+) $p$(cohort) | 1087.55 | 1.61 | 0.132 | 0.447 | 30 | 52.75 |
| $\Phi$(y1, y2, y3+) $p$(y1, y2, y3+*t) | 1087.57 | 1.62 | 0.131 | 0.444 | 21 | 72.03 |
| $\Phi$(y0-2, y3, y4+) $p$(y1, y2, y3+*t) | 1088.05 | 2.10 | 0.103 | 0.349 | 21 | 72.51 |

Figure 4.3. Adult Razorbill survival rates ($\Phi$) on the Gannet Islands [dark circles; $\Phi$(a1, a2+*t) $p$(pooled)] and Machias Seal Island (light circles) during 1996-2005, with 95% confidence limits. The best model for Machias Seal Island was one with constant survival ($\Phi$ = 0.967± 0.028). Here we present the time-dependent survival estimates from the global model [$\Phi$(y1, y2+*t) $p$(t)] for comparison purposes (see legend of Table 4.2 for explanation of subscripts).

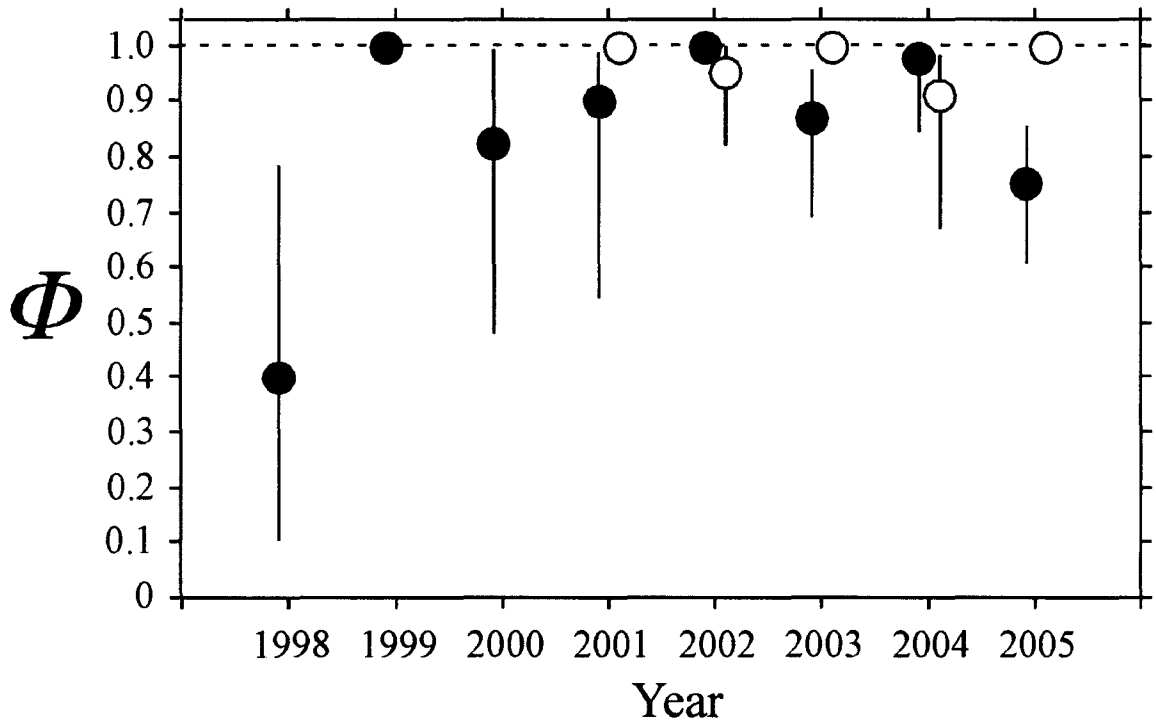

Table 4.6. Mean Razorbill survival estimates ($\Phi$) and their variability for the Gannet Islands and Machias Seal Island and some other colonies.

| Colony | Method | Age class | $\Phi$ | Years | Source |
|---|---|---|---|---|---|
| | | **Western Atlantic** | | | |
| Gannet Islands | Resight (metal bands) [a] | Pre-breeder (0-2 years) | 0.482±0.033SE | 1996-2003 | Present study |
| | | Age 3-11 years | 0.970±0.03SE | | |
| | | Banded as adult (3+ years) | 0.890±0.053SE | | |
| Machias Seal Island | Resight (metal bands) [a] | Pre-breeder (0-2 years) | 0.778±0.041SE | 1999-2006 | Present study |
| | | Age 3-8 years | 0.912±0.052SE | | |
| | | Banded as adult (3+ years) | 0.967±0.032SE | | |
| Quebec, Canada | Band recoveries and resightings [a] | Pre-breeder (0-5 years) | 0.380±0.04SE | 1925-1995 | Chapdelaine 1997 |
| | | Adult | 0.895±0.03SE | | |
| | | **Eastern Atlantic** | | | |

| | | | | | |
|---|---|---|---|---|---|
| Shiant Islands, Scotland | Resight [a, b] | Adult | 0.921 [d] | 1971-1977 | Steventon 1979 |
| Hornoya, Norway | Resight (metal and color bands) [a] | Adult | 0.919±2.5SD | 1995-2003 | Sandvik et al. 2005 |
| Britain & Irish Sea | Band recoveries [c] | Pre-breeder (0-4 years) | 0.570±4.8% | 1923-1971 | Lloyd 1974 |
| | | Adult | 0.890±1.0% | | |
| Isle of May, Scotland | Resight (color bands) [a] | Adult | 0.888±0.05SE | 1982-1987 | Harris and Wanless 1989 |
| Skokholm, Wales | Resight (metal and color bands) [a] | Pre-breeder (0-4 years) | 0.180 [d] | 1963-1973 | Lloyd and Perrins 1977 |
| | | Adult | 0.890±6.1SD | | |

[a] Survival probabilities estimated using CMR analysis.

[b] Band type (metal or color) not reported.

[c] Survival rates estimated using return rates (i.e. by dividing the number of marked individuals encountered in year $i + 1$ by the number marked in year $i$).

[d] Variation not reported.

# CHAPTER FIVE

# IMPACTS OF INTRASPCIFIC KLEPTOPARSITISM AND DIET SHIFTS ON RAZORBILL *ALCA TORDA* PRODUCTIVITY AT THE GANNET ISLANDS, LABRADOR

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## 1.1. ABSTRACT

Intraspecific kleptoparasitism, the stealing of food from members of the same species, has received widespread but mostly superficial attention in the scientific literature. However, the effects of such behavior can be significant. Here we report on high rates of intraspecific kleptoparasitism in the Razorbill (*Alca torda*) at the Gannet Islands, a behavior which appears to be colony specific. Razorbills carry their prey conspicuously in their bill making them vulnerable to kleptoparasitic attacks from neighboring birds. We examined the relationship between the frequency of kleptoparasitic attacks and the prey species carried by breeding adults. During 2003-2006, sixty nine percent of all Razorbills carrying food to their chick were attacked (n = 182) and of these attacks, 18% (n = 22) were successful. Group attacks (two or more kleptoparasites) were more successful numerically (27%, n = 71), however only one member of the group ever received the reward. The frequency of kleptoparasitism observed by Razorbills at the Gannet Islands is one of the highest reported for any seabird including many specialist kleptoparasites such as frigatebirds. This combined with the lowest observed Razorbill productivity (overall success = 0.40, n = 222) for the Gannet Islands and drastic shifts in diet may indicate decreased food availability.

## 2.1. INTRODUCTION

The stealing of food, or kleptoparasitism, is widespread among many seabird families, most prominently the Laridae, Fregatidae, and Stercorariidae (Hopkins and Wiley 1972, Carroll and Cramer 1985, Le Corre and Jouventin 1997, Spear *et al.* 1999, Shealer and Spendelow 2002). Kleptoparasitic behavior is separated into two forms: interspecific (between members of different species) and intraspecific (between members of the same species). In the family Alcidae, interspecific kleptoparasitism is relatively common (Ingold and Tschanz 1970, Rice 1985, 1987, Emms and Verbeek 1991, St. Clair *et al.* 2001); however, there have been few reported cases of intraspecific kleptoparasitism (Ainley *et al.* 2002).

Razorbills (*Alca torda*) are colonial seabirds that provision their chicks with small fish which they carry conspicuously in their bill (Hipfner and Chapdelaine 2002). Upon returning to the colony with fish, Razorbills typically land on one of a few roosting rocks adjacent to the breeding colony. Individuals must then walk from the roosting rock to the nest, which can be more than 20 feet away. During this time, individuals are vulnerable to kleptoparasitic attacks.

The frequency of kleptoparasitic interactions in many seabirds has been shown to respond to local conditions including decreasing prey availability (Uttley *et al.* 1994, Oro 1996, Ainley *et al.* 2002) and high rates of kleptoparasitism have been linked to decreased feeding rates and low productivity (Hulsman 1976, Sydeman *et al.* 1991, Barrett 1996, Tuckwell and Nol 1997, Triplet *et al.* 1999, St. Clair *et al.* 2001). Here we present the first record of high rates of intraspecific kleptoparasitism and discuss its potential relationship with Razorbill productivity and prey availability.

## 3.1. METHODS

### *3.1.1. Study site*

This study was conducted at the Gannet Islands, Labrador, Canada (53°56'N, 56°30'W), which include six islands (GC1-GC6) located in the Atlantic Ocean, approximately 40 kilometers northeast of Cartwright, Labrador. The Gannet Islands support the largest colony of Razorbills in North America with approximately 9,800 breeding pairs (Chapdelaine *et al.* 2001). In the 1980s the climate at the Gannet Islands was typical of the sub-Arctic region with heavy pack ice remaining around the islands until late-June (Birkhead and Nettleship 1983), however, the area has experienced significant warming in recent years and the water surrounding the islands are now completely clear of ice by as early as the first week of May (Canadian Ice Service 2006).

### *3.1.2. Chick diet and kleptoparasitism*

Observations of chick feedings were conducted from mid-July to late August in 1996 and from 2003-2006 from blinds located on islands GC2 and GC4. Kleptoparasitic interactions were recorded during feeding watches from 2003-2006. For each observed feeding or kleptoparasitic interaction the following information was recorded: the band number (when available) of the target (bird carrying the fish) and the kleptoparasite, the number, size, and species of fish involved, the number of birds involved in the attack, and the total number of times the target was attacked. In a successful attack, either the pursuer managed to grab the fish or part of it from the target's beak, or the target dropped the fish and the pursuer grabbed it just before or after it reached the ground. The success rate was defined as the number of attacks in which the kleptoparasite obtained food against the total number of attacks. In order to determine if a

particular fish species was preferred and therefore a bird carrying that species more likely to be attacked, we conducted binomial logistic regressions analyses.

*3.1.3. Productivity*

We used identical methods to those published by Birkhead and Nettleship (1983) for monitoring Razorbills at the Gannet Islands. Most Razorbills occupy crevices in low lying boulder-scree (<10m above sea level), so the presence of an egg or chick can only be detected by entering the colony and visiting individual nests. However, regular disturbance of Razorbill breeding sites has been shown to reduce breeding success (Birkhead and Nettleship 1983, Lyngs 1994), so we felt that these breeding sites may not provide a reliable estimate of Razorbill breeding success. A small proportion of the population breed on narrow cliff ledges and such sites can be monitored without disturbance as the occupant(s) were observed from a distance using a spotting scope or the naked eye. However, even this may not provide a good measure of breeding success since open sites are not typical of Razorbill nests on the Gannet Islands and are more vulnerable to gull predation (Birkhead and Nettleship 1983, Rowe and Jones 2000).

In order to accurately estimate Razorbill productivity and maintain comparable methods to those used by Birkhead and Nettleship (1983) we established three plot types that experienced varying levels of disturbance. Undisturbed plots were cliff sites which could be monitored without entering the colony. Low disturbance plots were checked only three times during the breeding season, once upon arriving on the islands in late June once all eggs had been laid, a second time when approximately 90% of eggs had hatched, and again 15 days later when the majority chicks were near fledging. Moderately disturbed plots were checked every 4 days beginning approximately 4 days prior to peak hatching and continuing until all chicks had fledged.

Moderately disturbed sites were not checked during incubation as Lloyd (1979) showed that in Razorbills most nest failure occurs during the incubation period.

Hatching success is defined as the proportion of eggs laid which produced chicks. Fledging success is defined as the proportion of chicks that survived to nest departure (not equivalent to fledging success which occurs at sea, Hipfner and Chapdelaine 2002). Overall success is the proportion of eggs laid that produced chicks that survived to 15 days of age.

## 4.1. RESULTS

### *4.1.1. Chick diet*

Sand lance (*Ammodytes* spp.) was consistently the dominant species representing more than 50% of the overall chick diet in all years of this study (Table 5.1). From 1996 to 2006, the proportion of adult capelin increased from 3% to 14% of the overall diet. Young of the year (YOY) capelin, a species not previously reported in the diet of Razorbills at the Gannet Islands, accounted for 3% of the overall diet in 2005 and 2006.

### *4.1.2. Productivity*

Razorbill reproductive success at the Gannet Islands was significantly lower in 2004 and 2005 than in any other year studied ($G = 64.17$, $df = 6$, $p < 0.001$; Table 5.2). Hatching success for 2004 and 2005 averaged 56% with nests in the low disturbance plot having the lowest value of 50% (Table 5.2, Table 5.3). Fledging success averaged 71% with nests in the low disturbance plot having the lowest value of 64% and the moderate disturbance and undisturbed plots being

78% and 73% respectively. Fifty-seven percent of chicks (n = 126) died within the first 7 days of life.

*4.1.3. Intraspecific kleptoparasitism*

Intraspecific kleptoparasitism in Razorbills at the Gannet Islands appears to be a recent phenomenon as no observations of this behavior have been reported since monitoring began in the early 1980s. This behavior was not observed at other colonies in Labrador or on Gull Island, NL (47°15'N, 52°46''W, J. Lavers, pers. obs.) and occurs only in about one out of every 60 feedings on Machias Seal Island (n = 221, UNB-ACWERN unpublished data).

A total of 182 observations of Razorbills carrying fish on the Gannet Islands were recorded from 2003 to 2006 (Table 5.4). Of these, 125 observations involved kleptoparasitic interactions in which the bird carrying the fish was attacked one or more times (attack rate = 0.69, Table 5.4). Sand lance, which accounted for more than 77% of all kleptoparasitic interactions, was significantly more likely to be the target of an attack compared to adult capelin and daubed shanny ($G = 8.17$, $df = 1$, $p = 0.004$). Overall, 18% of attacks were successful (n = 22).

Sixty six kleptoparasitic interactions involved two or more Razorbills attempting to steal fish from a single individual (referred to as mobbing from this point on). Mean group size was 4.3 birds (n = 71, SE = 0.30), however, in six cases 10 or more aggressors converge on the target bird from multiple directions. Nineteen of the 71 mobbings were successful (success rate = 0.27).

Twelve banded Razorbills were identified as the aggressor in kleptoparasitic interactions (Table 5.5). Eight of these birds were banded as chicks (known age). Mean age of the attacker was 4.8 years (range 3-8 years, SE = 0.74). The remaining four birds were banded as adults, so their exact age in unknown. However, previous studies have shown that the first bill groove does not develop until the third summer and increase by a maximum of one groove annually (Hipfner and Chapdelaine 2002, Hope Jones 1988); therefore these birds were 4 or more years of age. Eleven banded birds were identified as the target of kleptoparasitic attacks (Table 5.6), all of which were at least 5 years of age when the attack occurred. Since the number of Razorbills banded on the Gannet Islands was small compared to the total population size, it was not possible to determine if certain banded birds were specializing in kleptoparasitic behavior or were repeatedly the victim of attacks. All birds listed in Tables 5.5 and 5.6, except 895-13523 which was both an aggressor and a target, were observed in kleptoparasitic interactions only a single time.

In Razorbills, more than one nest can be found under a single boulder; therefore it is difficult to determine which nest an adult occupies once it has disappeared into a crevice. As a result, determining feeding rates and quantifying any direct effects of kleptoparasitism (i.e. reduced chick growth) was not possible in this study.

## 5.1. DISCUSSION

Razorbill diet at the Gannet Islands has shifted dramatically since the early 1980s with once dominant fish species such as capelin decreasing substantially in representation. In the early 1980s, capelin accounted for almost 40% of Razorbill chick diet at the Gannet Islands (Birkhead & Nettleship 1983, Table 1). By the mid 1990s, capelin were observed in only 3% of feedings,

indicating that a major shift had occurred. At the same time, Common Murres *Uria aalge*, Thick-billed Murres *U. lomvia*, and Atlantic Puffins *Fratercula arctica* at the Gannet Islands were all observed feeding their chicks up to 75% fewer capelin than in previous years (Bryant *et al.* 1999, Baillie & Jones 2004). It has been suggested that few alternatives to capelin exist in the prey base in Labrador and that without capelin, breeding failure of many seabirds is inevitable (Brown & Nettleship 1984). In the present study, the proportion of capelin in Razorbill chick diets increased slightly to 14%, however, the appearance of previously unrecorded prey items such as YOY capelin and an increase in daubed shanny *Lumpenus maculates* suggest that Razorbills were having difficulty locating capelin, and were turning to alternative (possibly less nutritious) prey.

Razorbill productivity at the Gannet Islands during 2004-2006 was the lowest recorded since monitoring began (Table 2). Hatching success was especially low being only 62% compared with 87% and 70% for Razorbills monitored on Machias Seal Island in the same years (Bond *et al.* 2007). Razorbill fledging success typically ranges between 85-95% (Lloyd 1979, Harris and Wanless 1989, Lyngs 1994, Hipfner and Bryant 1999), but on the Gannet Islands was only 63%. Chick mortality is typically greater in the first few days of life due to an inability to thermoregulate (Barrett 1984). In our study, however, 43% of chick mortalities were of late stage chicks (8-12 days old) with no obvious cause of death other than emaciation. Although some Razorbills successfully raised chicks, fledging success was low. It appeared that prey alternatives to capelin were available to Razorbills at the Gannet Islands, but they may not have been sufficiently abundant or energetically equivalent. These findings provide partial support for

Brown and Nettleship's (1984) hypothesis that prolonged absence of capelin leads to reduced reproductive performance of seabirds in Labrador.

Poor productivity in Razorbills at the Gannet Islands did not appear to be associated with human disturbance in 2004-2006. This conflicts with Birkhead & Nettleship's (1983) study of Razorbill productivity at the Gannet Islands, which found that regular researcher visits to breeding sites significantly reduced hatching success. In both years of our study, productivity in sites checked only a few times throughout the breeding season (low disturbance) was significantly lower than plots checked at 4-day intervals (moderate disturbance). The low disturbance plot was changed from 2004 to 2005, which reduced the possibility of having chosen a particularly poor site in both years. Cliff nesting Razorbills (undisturbed plot) had the highest success rate, despite increased exposure to gull predation and weather.

The level of kleptoparasitism observed in Razorbills at the Gannet Islands was among the highest reported for seabirds, including many specialist or habitual kleptoparasites such as frigatebirds, gulls, and terns (Osorno *et al.* 1992, Steele & Hockey 1995, Shealer & Spendelow 2002, Martinez-Abrain *et al.* 2003). Overall, attacks performed by single Razorbills were less successful than those carried out by groups. The greater success rate of group attacks appeared to result from an enhanced ability to harass and overwhelm the target, as has been reported for Arctic Skuas *Stercorarius parasiticus* (Arnason & Grant 1978). However, only one individual in the group ever received the stolen fish; thus the success rate per individual decreased as the number of participants in the group increased (see also Hatch 1975, Caldow & Furness 2001). In Razorbills, an average group size of less than 2 individuals was required to make the per-capita

rate of success from group attacks equal to that of individual chases. Mean group size in Razorbills is 4.3 individuals; therefore there were very few circumstances in which individuals could increase their chance of success by joining a group. The fact that we observed as many as 15 individuals competing for a single fish adds further support to the idea that food availability was low during this study.

In many seabirds, immature birds are more likely to kleptoparasitize than adults (Carroll & Cramer 1985, Steele & Hockey 1995, Tuckwell & Nol 1997). Breeding adults are typically more experienced foragers, so juveniles are able to use intraspecific kleptoparasitism to exploit the greater hunting capabilities of adults (Steele & Hockey 1995). However, this was not the case for Razorbills, as all but 3 banded birds (n = 23) involved in kleptoparasitic interactions were of breeding age at the time the attack occurred. The fact that experienced breeders are attempting to steal food from other breeders rather than forage on their own may further indicate that food availability was low.

In some seabird species, behavioral shifts such as an increase in kleptoparasitic activity have been linked to low prey availability (Steel & Hockey 1995, Triplet 1999, Ainley *et al.* 2002,). For Razorbills, this also appears to be the case. The appearance of YOY capelin in the diet of Razorbills and high rate of kleptoparasitism may be a result of increasing sea surface temperatures (Petrie *et al.* 2003, Petrie *et al.* 2004) and decreased food availability. Capelin and sand lance are cold water species (Carscadden *et al.* 2001), and independent of their actual abundance, may become less available to Razorbills when they migrate down the water column away from warmer surface waters (Methven & Piatt 1991).

Furness (1987) found that the proportion of birds successfully attacked by kleptoparasites was always less than 5% in a number of seabird species and suggested that relatively low impact is a necessary condition for the interaction of kleptoparasites and targets to be evolutionarily stable. The success rate for individual Razorbill kleptoparasites (not including mobbings) was almost three times the level that might be considered sustainable. If the same individuals are consistently delayed in feeding their chicks, the survival of the young will be reduced (Hulsman 1976). Thus, the level of kleptoparasitism we observed is potentially detrimental and may explain the low rate of productivity in Razorbills. Future studies should attempt to quantify directly the impacts of kleptoparasitism on chick feeding and growth rates since, because consistently low productivity resulting from kleptoparasitism could lead to population declines in the long-term.

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Table 5.1. Diet of Razorbills at the Gannet Islands, Labrador, 1981-2006. Percentage composition based on number of items delivered.

| Years | 1981-1982 | 1996 | 2003-2006 |
|---|---|---|---|
| Source | Birkhead and Nettleship 1983 | Jones, unpublished data | Current study |
| Prey type | | | |
| Sand lance | 0.62 | 0.90 | 0.80 |
| Capelin, adult | 0.38 | 0.03 | 0.14 |
| Capelin, YOY [a] | 0.00 | 0.00 | 0.03 |
| Daubed Shanny | <0.01 | 0.01 | 0.03 |
| Other | 0.00 | 0.06[b] | 0.00 |

[a] Young of the year

[b] Other species include stout eelblenny *Anisarchus medius*, snakeblenny *Eumesogrammus praecisus*, and squid

Table 5.2. Razorbill productivity at the Gannet Islands, Labrador, 1980-2006.

| Years | 1980-1983 | 1997 | 2004-2006[a] |
|---|---|---|---|
| Source | Birkhead and Nettleship (1983) | Hipfner and Bryant (1999) | Current study |
| Hatching success (%) | 492/775 (0.63) | 38/51(0.75) | 196/314 (0.62) |
| Fledging success (%) | 377/492 (0.77) | 37/38(0.97) | 125/197 (0.63) |
| Overall success (%) | 377/775 (0.49) | 37/51 (0.73) | 125/314 (0.39) |

[a] Nests from each of the three different plot types (low disturbance, moderate disturbance, and undisturbed) are combined

Table 5.3. Breeding success of Razorbills at the Gannet Islands in two disturbed and one undisturbed plot, 2004 to 2006.

| Plot Type | Hatch Success (%) | Fledge Success (%) | Overall (%) |
|---|---|---|---|
| No disturbance | 46/61 (0.75) | 28/46 (0.61) | 28/61 (0.45) |
| Low Disturbance | 72/130 (0.55) | 43/72 (0.60) | 43/130 (0.33) |
| Moderate Disturbance | 79/123 (0.64) | 54/79 (0.68) | 54/123 (0.44) |
| Total | 196/314 (0.62) | 125/197 (0.63) | 125/314 (0.39) |

Table 5.4. Fish species involved in kleptoparasitic interactions between Razorbills on the Gannet Islands from 2003-2006.

| Prey type | Number of birds carrying fish | Number of birds attacked (%) | Number of successful attacks (%)[a] |
|---|---|---|---|
| Sand lance | 127 | 91 (0.72) | 17 (0.19) |
| Capelin, adult | 23 | 11 (0.48) | 4 (0.36) |
| Capelin, YOY | 6 | 4 (0.67) | 0 (0.00) |
| Daubed Shanny | 10 | 3 (0.30) | 0 (0.00) |
| Unidentified | 16 | 15 (0.94) | 1 (0.07) |

[a] Fish was stolen by kleptoparasite

Table 5.5. Razorbills that were the aggressor in kleptoparasitic interactions on the Gannet Islands. Number of bill grooves is provided for birds banded as adults.

| Band Number | Year Banded | Year involved in kleptoparasitic interaction | Minimum age at time of attack | Number of Bill Grooves | Attack successful? |
|---|---|---|---|---|---|
| 895-13523 | 1997 | 2006 | 11 | N/A | Unknown |
| 895-13851 | 1997 | 2006 | 11 | N/A | No |
| 895-13999 | 1997 | 2005 | 8 | N/A | Yes |
| 895-14436 | 2000 | 2006 | 6 | N/A | No |
| 895-14439 | 2000 | 2003 | 3 | N/A | Yes |
| 895-15780 | 1998 | 2005 | 7 | N/A | No |
| 895-15831 | 2000 | 2006 | 6 | N/A | Yes |
| 895-18412 | 2003 | 2006 | 3 | N/A | Yes |
| 895-18429 | 2003 | 2006 | 3 | N/A | Yes |
| 895-18436 | 2003 | 2006 | 3 | N/A | No |
| 895-19726 | 2005 | 2005 | 4 | 2 [a] | No |
| 895-19729 | 2005 | 2005 | 5 | 3 [a] | No |

[a] See text for explanation

Table 5.6. Razorbills that were victims of kleptoparasitic attacks on the Gannet Islands. Number of bill grooves is provided for birds banded as adults.

| Band Number | Year Banded | Year involved in kleptoparasitic interaction | Minimum age at time of attack | Number of Bill Grooves | Fish Stolen? |
|---|---|---|---|---|---|
| 895-13168[a] | 1996 | 2004 | 8 | 1.5 | No |
| 895-13266 | 1996 | 2004 | 8 | N/A | Yes |
| 895-13412 | 1996 | 2005 | 9 | N/A | No |
| 895-13526 | 1997 | 2005 | 8 | 2 | No |
| 895-13523 | 1997 | 2006 | 9[b] | N/A | No |
| 895-13856 | 1997 | 2006 | 9[b] | 2 | Yes |
| 895-15978 | 2002 | 2003 | 3[b] | 1 | No |
| 895-16559 | 2001 | 2003 | 4[b] | 2 | No |
| 895-17921 | 2004 | 2006 | 5[b] | 2 | Unknown |
| 895-19418 | 2004 | 2006 | 5[b] | 2.5 | Yes |
| 895-19725 | 2005 | 2005 | 4[b] | 2 | No |

[a] 895-13168 was recaptured as an adult in 2000

[b] See text for explanation

# CHAPTER SIX

# FACTORS AFFECTING POPULATION DYNAMICS OF THE RAZORBILL *ALCA TORDA* AT TWO BREEDING COLONIES IN ATLANTIC CANADA

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## 1.1. ABSTRACT

We developed a deterministic age based matrix projection population model to assess population viability and quantify the impact of mortality caused by illegal hunting and fox predation on Razorbill *Alca torda* populations breeding on the Gannet Islands, Labrador (impacted population) and Machias Seal Island, New Brunswick (un-impacted population). We estimated the potential population growth rate in the absence of anthropogenic mortality sources by using pre-breeder survival estimates from the relatively unaffected Machias Seal Island Razorbill population. We used data collected on fox predation on the Gannet Islands from 1978 to 2006 to estimate the change in fecundity as a result of fox presence. The intrinsic growth rate ($\lambda$) of the deterministic matrix based on vital rates from the Gannet Islands was 0.9475 and for Machias Seal Island was 1.0613. Hunting mortality reduced the Gannet Islands population growth rate by 0.0603, while fox predation reduced population growth rate by 0.0126. Combined these sources reduced the population growth rate by 0.0729. Although the Razorbill population on Machias Seal Island appears to be growing rapidly, without substantial immigration the Gannet Islands population may be declining, likely due to illegal hunting. Recommendations for the conservation and protection of Razorbills on the Gannet Islands are discussed.

## 2.1. INTRODUCTION

Understanding the life-history strategies and responses of organisms to natural and anthropogenic mortality is essential to the proper management of populations. The ability to quickly detect adverse changes to populations and determine the possible cause is critical, but challenging in some species (Croxall and Rothery 1991). In seabirds, low reproductive rates and delayed breeding can make it difficult to detect changes in breeding success, population size, and survival. Since reductions in survival of even a few percentage points can have large effects on the lifetime reproductive success of individuals and populations as a whole (Merkel 2004, Sandvik et al. 2005), identifying the factors responsible for population declines is a key objective of conservation oriented studies. To do this, researchers are increasingly turning to demographic models that identify key life stages or sources of mortality influencing populations (Lebreton and Clobert 1991, McDonald and Caswell 1993). Such models, generally referred to as population viability analyses (PVA; Morris and Doak 2002), can also be used to assess the effectiveness of different management strategies and guide future research. For seabirds, models have been developed to address issues such as bycatch of adults in fisheries, hunting, and introduced predators (Hamilton and Moller 1995, Cuthbert et al. 2001, Velando and Freire 2002).

Most seabirds breed on remote islands, and as such, have few predators other than man (Larson 1960, Lack 1968, Croxall and Rothery 1991). However, native mammalian predators such as Arctic foxes *Alopex lagopus* are able to reach some islands by traveling over pack ice (Larson 1960, Birkhead and Nettleship 1995). The presence of even a single fox around some seabird colonies has resulted in delayed and asynchronous breeding and in many cases, complete abandonment of the breeding site (Larson 1960, Southern et al. 1985, Ratcliffe et al. 2000,

Samelius and Alisauskas 2001). At the Gannet Islands, Labrador most Razorbills *Alca torda* breed in low-lying crevices and under boulders that are accessible to Arctic foxes. In years where foxes were present, only a few individuals nesting on steep, inaccessible cliffs and ledges bred successfully (Birkhead and Nettleship 1995, Rowe and Jones 2000). Birkhead and Nettleship (1995) quantified the level of predation by foxes and response of Razorbills to their presence on the Gannet Islands. However, the effects of repeated years of fox predation and reproductive failure on the long-term status of the Razorbill population on the Gannet Islands remain unknown.

In Newfoundland and Labrador, hunting of seabirds for sustenance and recreation is common and has been a significant threat to some populations (Blanchard 1984, Chardine et al. 1999). Each year from September to April, residents of Newfoundland and Labrador legally hunt 350,000 or more Common *Uria aalge* and Thick-billed Murres *U. lomvia* (Elliot 1991). Razorbills are classified as a non-game species, so there is no open hunting season (Labrador Inuit are permitted to legally hunt Razorbills under the Migratory Birds Convention Act; Chardine et al. 1999, Chapdelaine et al. 2001), but due to their close physical resemblance to the murres, many hundreds to thousands of Razorbills are accidentally or deliberately shot each year (Elliot 1991, Chapdelaine 1997). The North American Razorbill population is small (less than 38,000 pairs, Chapdelaine et al. 2001) and has declined historically in many parts of its range as a result of hunting, egging, and disturbance to breeding colonies (Blanchard 1984, Nettleship and Evans 1985). During the 1980s and 1990s, Razorbill populations in North America appeared to be increasing (Robertson and Elliot 2002, Robertson et al. 2002). However, recent census data is lacking and demographic studies conducted at their largest North American colony, the Gannet

Islands, Labrador, suggest that population parameters, including productivity and adult survival, have declined over the past 20 years (see Chapters 4 and 5). Here we develop a population model to examine the status of the Gannet Islands Razorbill population in relation to the relative and cumulative effects of mortality due to fox predation and hunting bycatch, and compare the results with an unaffected population breeding on Machias Seal Island, New Brunswick.

## 3.1. METHODS

### *3.1.1. Study sites*

Demographic data were collected on the Gannet Islands, Labrador, Canada (53°56'N, 56°30'W, Figure 6.1) and Machias Seal Island, New Brunswick, Canada (MSI, 44°3'N, 67°06'W) from 1995-2006 in connection with a long-term study on the survival and status of Atlantic Canadian Razorbill populations. The Gannet Islands cluster includes six islands (GC1-GC6) which support the largest colony of Razorbills in North America (c. 9,808 breeding pairs; Chapdelaine et al. 2001). From approximately December to April, the waters surrounding the Gannet Islands are almost completely covered in pack ice (Canadian Ice Service 2006). MSI, a small island located approximately 10 km off the coats of Maine, supports 543 Razorbills pairs which have been closely monitored since 1995 (Grecian 2005).

### *3.1.2. Demography*

Razorbills exhibit a life-history strategy typical of most long-lived seabirds with low fecundity, high adult survival, and delayed breeding. Razorbill demographic parameters were estimated on the Gannet Islands and Machias Seal Island during 1995-2006 (see Chapters 3 to 5) and are presented in Table 6.1. Three additional studies examined Razorbill productivity on the Gannet

Islands during 1980-1983 and in 1997 and reported substantially higher productivity values (from 0.47 to 0.73) compared to the current estimate of 0.39 for 2004-2006 (Birkhead and Nettleship 1983, Hipfner and Bryant 1999, **Rowe and Jones 2000**). The Gannet Islands Razorbill population grew by more than 20% during this time, either through immigration or intrinsic factors, despite experiencing both hunting pressure and fox predation (Robertson and Elliot 2002). Using the current survival and age at first breeding estimates presented in Table 6.1, we ran a model that incorporated productivity values from these past studies to determine if the observed population increase seen in the 1980s and 1990s could be replicated.

*3.1.3 Mortality due to foxes*

We used records of fox presence on the Gannet Islands from 1978 to 2006 to estimate the probability that a fox will be present on one or more of the islands in a given year (Table 6.2). Of 17 years surveyed, foxes were present in nine years; therefore we assumed that a fox will be present on the at least one of the islands once out of every two years.

Birkhead and Nettleship (1995) estimated that 2,555 Razorbills nests were abandoned on GC2, GC4, and GC5 in 1992 due to the presence of foxes (Table 6.3). Five adult Razorbills were also found predated by the foxes (Birkhead and Nettleship 1995). The data presented in Birkhead and Nettleship (1995) likely overestimate the average number of breeding sites predated or abandoned in a given year since foxes were present on three of the six islands in 1992. I.L. Jones, J.W. Chardine and R.D. Elliot visited GC2 and GC4 (only) in 1995 and found foxes present, breeding sites abandoned, and many corpses of adult Razorbills (personal observations). In order to determine the potential number of nests lost due to a fox in an average year (when

foxes are located on only one of the six islands, Table 6.3), we estimated the mean number of Razorbill nests (1635± 435) based on counts for each of the six islands in the cluster. Assuming that all nests on an island are abandoned or predated when a fox is present, this results in a 17% (1635/9808 breeding pairs = 0.167) reduction in the breeding population. Overall fecundity in years with no foxes is 0.39 (see Chapter 5) and is 0.32 (7% reduction) when a fox is present. This value was used in all population models.

*3.1.4. Mortality due to hunt*

Recoveries of Razorbills banded on the Gannet Islands from 1996-2005 were examined to determine age structure and any temporal or spatial bias in the distribution of the recoveries.

An analysis of band recoveries for Razorbills banded in Quebec during 1925-1994 suggested that several hundred to thousands of Razorbills were shot accidentally in the hunt each year (Chapdelaine 1997) and interviews with hunters suggested that approximately 5% of the annual take of murres are actually Razorbills (Elliot 1991). The total annual harvest of murres in Newfoundland and Labrador was estimated at 173,000 during 2001-2003 (Canadian Wildlife Service unpublished data). Using the Razorbill bycatch estimate provided by Elliot (1991), the estimated number of Razorbills shot during the hunt is approximately 8,650 per year. However, not all of these birds would have originated from the Gannet Islands. The Gannet Islands population accounts for almost 30% of the North American population, therefore using Elliot's (1991) estimate of 5% bycatch, this suggests that as many as 2,595 Gannet Islands Razorbills are shot.

*3.1.5. Population model*

We developed a deterministic, age-structured, post-breeding, Lefkovitch population projection matrix similar to that used by Wiese et al. (2004) for Thick-billed Murres. The computer model written in Matlab (version 13, MathWorks Inc.) consisted of eight age classes, and only females were considered. Fecundity parameters in Table 6.1 were divided by 0.5 assuming a 1:1 sex ratio. Based on age at first breeding data for the Gannet Islands and Machias Seal Island, we define breeding birds as four years and older (J. Lavers, unpublished data).

The effects of anthropogenic mortality (and in this case, fox predation) are most easily determined by comparing survival rates between affected and unaffected populations (Wiese et al. 2004). However, few populations are unaffected by anthropogenic mortality, therefore studies comparing affected and unaffected populations are rare. For this study, we were fortunate enough to have demographic data for a putative unaffected Razorbill population on Machias Seal Island (Chapdelaine et al. 2001) and were able to quantify the effects of hunting bycatch on pre-breeder survival.

We evaluated the individual and cumulative effects of hunting mortality and Arctic fox predation on population dynamics in two phases. First, we determined the baseline growth rates for the Gannet Islands (affected) and MSI (unaffected) Razorbill populations using vital rates estimated during 1995-2006. Second, to account for birds killed during the hunt, we ran the same model using pre-breeder survival estimates from MSI and the resulting change in the population growth rate was determined. Since fecundity estimates for the Gannet Islands were based on data from islands which did not experience fox predation, it was not necessary to account for this mortality.

In phase one, we determined the stable age distribution (w), the elasticity matrix (e), and the intrinsic growth rate of the deterministic matrix over 20 years ($\lambda$; Caswell 2001). A deterministic approach was preferred since modeling variation in the demographic parameters (i.e. a stochastic projection) can slow the population growth rate over the long term and can represent an even worse case scenario for populations that are thought to be declining (Fiedler and Kareiva 1998, Jones 2002, Morris and Doak 2002). We chose a 20 year time interval as it is most relevant from a management perspective and allowed us to overlook density-dependent processes associated with long-term projections (Wiese et al. 2004). We used elasticity analysis of the matrix projection models to identify the vital rate that had the largest proportional impact on the population growth rate (Morris and Doak 2002).

In phase two, we examined the impact of fox predation and hunting mortality on population dynamics. We did this by incorporating a 7% reduction in productivity in every second year due to the presence of a fox and comparing the population growth rate to the baseline (i.e. no foxes). To estimate the effect of hunting we substituted the Gannet Islands pre-breeder survival rate with MSI and projected the population ahead 20 years. We then estimated the number of birds that had to be removed each year (i.e. killed in the hunt) to lower the population growth rate back to the baseline value determined in phase one. Relative decreases in the population growth caused by each mortality factor as well as the cumulative effects of both impacts were calculated.

## 4.1. RESULTS

### *4.1.1. Razorbill recoveries*

We obtained band recoveries for 23 Razorbills banded as chicks on the Gannet Islands during 1996-2005. The month of recovery and location were not known for three of these birds; therefore they are excluded from the data set. Ninety percent of Razorbill recoveries (n = 20) occurred between October and December, months during which the highest numbers of murres are harvested by hunters in Newfoundland and Labrador (Figure 6.1; Elliot 1991). Band returns of shot Razorbills were likely deterred by the fact that hunting Razorbills is illegal (anonymous hunters, pers. comms.). Recovery locations are shown in Figure 6.2. All birds recovered in Labrador (n = 4) were shot in the first two weeks of October suggesting that some birds may remain in the area for up to two months following fledging. Recoveries of the 16 remaining birds are all concentrated along the southeastern tip of Newfoundland suggesting that Razorbills follow a southward movement along the east coast of Newfoundland to their wintering grounds (Figure 6.4). Overall, first-year birds had a higher rate of recovery than birds two years of age or older (Table 6.4). Mean age of recovery was 112 ±17 days (n = 20). All 23 recoveries were direct (i.e. banded bird killed or found dead before, during, or immediately following the first period of migratory movement following banding and before return migration would likely have occurred; Gustafson et al. 1997) except one bird that was banded in August 2001 and recovered in February 2003.

*4.1.2. Baseline*

The intrinsic growth rates of the deterministic matrix for the Gannet Islands and MSI using current demographic parameters estimated for each population were $\lambda = 0.9475$ and $\lambda = 1.0613$ respectively (Table 6.5). Assuming stable age distribution, 57% of individuals in the Gannet Islands and MSI populations were breeders (Figure 6.3). Proportional changes (elasticity) in

survival of breeding birds (7+ years of age) had the largest influence on population trends, 0.6195 for the Gannet Islands and 0.5124 for MSI (Figure 6.4). Pre-breeder survival (0-2 years), survival of birds age 3-6 years, and fecundity all had a weaker influence on $\lambda$ compared to adult survival (Figure 6.4).

*4.1.3. Mortality model*

In our model, the Gannet Islands population growth rate declined by 0.0126 to $\lambda = 0.9952$ due to fox predation (Table 6.5). Pre-breeder survival on the Gannet Islands was 0.482 and on MSI is 0.778. In the absence of hunting bycatch, we assumed that pre-breeder survival on the Gannet Islands would be similar to MSI. Therefore using MSI pre-breeder survival (i.e. no hunting effect) and in the absence of fox predation, the Razorbill population on the Gannet Islands is expected to grow at $\lambda = 1.0078$ per annum (Table 6.5). Since accurate estimates of the number of Razorbills shot from the Gannet Islands are not available, we estimated annual bycatch by determining the number of Razorbills that must be shot to reduce the growth rate from $\lambda = 1.0078$ to the current value of $\lambda = 0.9475$. We determined that 1,400 individuals must be shot per year (these value were multiplied by 0.5 to only include females; Table 6.5) from the Gannet Islands to lower the growth rate to approximately 0.9475. Using Elliot's (1991) estimate of 5% bycatch (n = 2,595 birds shot per year), the Gannet Islands Razorbill population declined to extinction in only 10 years ($\lambda = 0.9211$; Table 6.5). Using the mean of the three past productivity estimates (Birkhead and Nettleship 1983, Hipfner and Bryant 1999, Rowe and Jones 2000), the Gannet Islands population growth rate was 1.0239 (Table 6.5).

## 5.1. DISCUSSION

### *5.1.1. Model assumptions*

In our models we assumed that Razorbill populations on the Gannet Islands and MSI were not near carrying capacity, therefore density-dependent factors were not limiting the populations. Here we provide evidence to support this assumption. Census data for the Gannet Islands Razorbill population indicate that the population increased from approximately 6,497 pairs in 1978 to 9,808 pairs in 1999 (Robertson and Elliot 2002). However, during 2003-2006 Razorbills bred at unusually low densities at some sites on the Gannet Islands (see Table 6.3, plots GC2-b and c) and what appeared to be suitable breeding sites (i.e. breeding site was occupied in previous years) were unoccupied (J. Lavers, pers. obs.). In the Gulf of Maine, Razorbill populations were locally extirpated and have only recently begun to recover (Hipfner and Chapdelaine 2002, also see Chapter 3) and all populations are small (<800 pairs). We believe these observations support the assumption that the North American Razorbill population is not currently at carrying capacity. Therefore density-dependent processes at breeding sites and at sea were likely not a concern in the short-term. It is possible that Razorbills breeding on MSI may begin to experience density-dependent effects in the next 20 years based on the population trajectory (see more below), however this will depend on whether birds from MSI continue to disperse and recruit to adjacent islands in the Gulf of Maine (see Chapter 3).

A critical assumption in the construction of demographic models concerns whether harvest mortality is compensatory or additive (Aebischer et al. 1999, Moller 2006). Anthropogenic mortality (i.e. hunting) is in some cases, at least partially additive to natural mortality and is responsible for slowed growth or decline of populations (Wiese et al. 2004, Moller 2006).

However, the extent to which hunting is additive can depend on a number of factors including the timing and intensity of the hunt as well as age of the birds taken (Ebbinge 1991, Madsen 1995, Dehorter and Tamisier 1998, Kokko 2001). The compensatory mortality hypothesis assumes that hunting kills the "doomed surplus" (Nichols 1991, Boyce et al. 1999). In other words, hunting removes individuals from the population that would be killed anyway due to density-dependent processes typical of populations near carrying capacity (Nichols 1991, Boyce et al. 1999). However, the observed 30% difference in pre-breeder survival between the Gannet Islands and MSI (see Chapter 4 and Table 6.1) is extremely large and hard to explain on the basis of the compensatory mortality hypothesis given that neither population is near carrying capacity (Nichols 1991).

*5.1.2. Fox predation*

The deliberate introduction and natural invasion of foxes on islands free of mammalian predators can have devastating and long-lasting effects on seabird colonies (Larson 1960, Petersen 1982, Bailey and Kaiser 1993). Over the last 30 years, Arctic foxes that crossed the winter ice to the Gannet Islands have had severe impacts, killing adult Razorbills and markedly reducing the number of birds attempting to nest (Birkhead and Nettleship 1995). The result of our study show that the presence of foxes on the Gannet Islands reduced Razorbill productivity by approximately 7%, resulting in a 1.26% decrease in the population growth rate. This mortality is likely underestimated as our model did not incorporate any adult Razorbill mortality as a result of fox predation (even though this was observed in 1992 and 1995) and did not account for years when foxes are present on more than one island in the cluster.

In the Baltic, the invasion of feral mink *Mustela vison* lead to a drastic decrease in the number of Razorbill colonies and resulted in an almost complete redistribution of the colonies as birds moved to increasingly remote, mink-free islands (Nordstrom and Korpimaki 2004). Fortunately, the removal of mammalian predators, including foxes, has been shown to significantly increase hatching success and growth rate of many seabird populations (Cooper and Fourie 1991, Bailey and Kaiser 1993). Removal of the foxes on the Gannet Islands poses an ethical issue as the foxes are native, arriving on the islands naturally. In addition, the islands are listed as an Ecological Reserve under the *Wilderness and Ecological Reserves Act* (Section 24(3)(a)(ii)), therefore removal of the foxes is prohibited. Under normal circumstances, Razorbill populations would normally be able to sustain repeated years of low productivity as a result of fox predation due to high adult survivorship. However, adult and pre-breeder survival rates on the Gannet Islands are some of the lowest reported for any Razorbill colony (likely due in part to the hunt; see Chapter 4) and it is likely that without immigration from other islands (see Chapter 3), the population will decline.

One of the main objectives of the *Wilderness and Ecological Reserves Act* is to provide protection for rare species and their habitat. The Razorbill is one of the least abundant auks in the North Atlantic with the Gannet Islands accounting for 25% of the total North American population (Chapdelaine et al. 2001). We therefore recommend the development of a management plan for the Gannet Islands where foxes are removed each year in late May or early June before the birds begin to lay their eggs.

*5.1.3. Hunting mortality*

Gannet Islands Razorbill recoveries reported by Chapdelaine (1997) from 1925-1960 included two birds from the Gannet Islands that were recovered in the Gulf St. Lawrence, Quebec which suggested some movement through this area. However, from 1960-1994 Chapdelaine (1997) did not report further recoveries in the Gulf St. Lawrence and all Razorbill recoveries from the Gannet Islands from 1996-2005 were made along the east coast of Newfoundland and Labrador. When interpreting the recoveries, consideration must be given to any spatial or temporal bias in the timing and route of migration in relation to areas of high and low hunting pressure (Chapdelaine 1997). Hunting of seabirds is widespread throughout Newfoundland and Labrador; however the human population is heavily biased to Newfoundland providing a partial explanation for why 67% of recoveries were made along the east coast of Newfoundland. No systematic effort was made to obtain band recoveries during this period. We expected that the recovery rate for shot Razorbills is likely low because hunters are aware that it is illegal to kill Razorbills and thus avoid turning in bands. After four field seasons in Labrador, J. Lavers was able convince a small number of hunters to turn in their Razorbill bands on the condition that they could remain anonymous.

In general, young inexperienced murres and Razorbills are at the greatest risk of hunting even though they represent only 10-15% of the population (Chapdelaine 1997, Chardine et al. 1999). It has been suggested that young birds may winter closer to the coast, thus exposing them to hunting (Falk and Durink 1992, Chapdelaine 1997). Our data support this idea as 96% of birds recovered from 1996-2005 were less than one year of age and only one second year bird (age 434 days) was recovered. The age structure of Razorbill recoveries reported during 1996-2005

differs significantly from Chapdelaine (1997) for 1925-1994 ($\chi^2$ = 10.665, p = 0.005; Table 6.4). Specifically, there was a complete absence of recoveries of birds older than two years compared to 6% of recoveries of birds age 4+ during 1925-1994 (Table 6.4; Chapdelaine 1997).

The Gannet Islands baseline Razorbill population growth rate ($\lambda$ = 0.9475) predicts a declining population in the absence of immigration. In contrast, the MSI Razorbill population is increasing rapidly at around 6% per annum ($\lambda$ = 1.0613) and is projected to increase from the current 543 pairs to an estimated 3,120 pairs in the next 20 years. MSI is a small island and is likely not capable of sustaining a Razorbill population of this size. Razorbill band resightings in the Gulf of Maine suggest that many of the surplus birds from MSI are recruiting to other nearby islands (see Chapter 3), therefore MSI Razorbills may not experience density-dependent effects in the short-term.

We estimated that annual Razorbill pre-breeder survival at the Gannet Islands has been reduced by 6.03% as a result of bycatch in the murre hunt, which is approximately equivalent to 700 female Razorbills being shot each year. This estimate is higher than for Thick-billed Murres (2.0%; Wiese et al. 2004), but is comparable to estimates of annual oiling mortality in Razorbills (5.6%; Baillie and Mead 1982) and Harlequin Ducks *Histrionicus histrionicus* (5.7%; Esler et al. 2000). We feel that our estimate of hunting mortality is realistic based on recent information collected from hunters and band returns. For example, on two days in October 2005, two banded and 35 unbanded Razorbills were shot legally by two aboriginal hunters less than 200 km from the Gannet Islands (anonymous source). Elliot (1991) suggested that as many as 5% of the murres shot each year are actually Razorbills, however when this value was applied to the model,

the Gannet Islands Razorbill population declined to extinction in only 10 years. Therefore, we believe this estimate may be too high; however there may be some cases, depending on factors such as weather and timing of migration, where this estimate may apply. For example, in October 2004 two banded Razorbills were shot along with 18 murres (11% Razorbill bycatch; anonymous source) and in November 2006, two Razorbills were shot out of approximately 70 murres (3% Razorbill bycatch; S. Gilliland, pers. comm.). In November 1981, of 340 seabirds shot in Twillingate, Newfoundland, 63 (18%) were bycatch species (i.e. not murres), including four Razorbills (1.8%; Wendt and Cooch 1984).

*5.1.4. Conservation implications*

Our estimates of pre-breeder and adult survival on MSI (see Chapter 4) were the highest reported for any colony, suggesting that conditions in the Bay of Fundy are favorable. In contrast, adult and pre-breeder survival rates for the Gannet Islands were significantly lower, likely the result of hunting, but also possibly the result of poor feeding conditions (and therefore fledgling condition, see Chapter 5) and dispersal outside the sampling area (see Chapter 3). Therefore, our use of the MSI pre-breeder survival rate may slightly over estimate the level of hunting mortality experienced by Razorbills from the Gannet Islands. However, we have neglected to consider other recognized sources of mortality for Razorbills in our model due to lack of sufficient, recent data, but identify these issues in the following paragraphs.

In addition to hunting mortality and fox predation, bycatch of Razorbills in fisheries and mortality due to oiling are also threats to the population. Most Razorbills taken in the harvest are juveniles (Table 4.4; Chapdelaine 1997); however, industrial fisheries and oil are non-selective

sources of mortality that affect both adult and immature birds (Belda and Sánchez 2001, Wiese et al. 2004). Although a moratorium on fishing was put in place in 1992, some fishing continues in Newfoundland and Labrador and it is likely that the moratorium may be lifted in coming years. Fishing poses a serious threat to Razorbills that specialize in under-water pursuit diving to catch their prey and they become entangled in gillnets and drown (Stran et al. 1991, Murray et al. 1994). Piatt and Nettleship (1987) estimated that 12.4% of the Newfoundland Razorbill population drowns each year in gillnets. This rate of bycatch is more than triple that found for Razorbills in Finland (3.4%, Bakken and Falk 1998) and exceeds the annual adult mortality for stable populations.

While at sea, Razorbills are exposed to oil pollution and although there have been no major oil spills at the Gannet Islands, the Terra Nova spill in Newfoundland in 2004 and chronic oil pollution produced from illegal dumping have caused significant oiling mortality in other auk species (Baillie and Mead 1982, Wiese 2002, Wiese and Ryan 2003, Wilhelm et al. 2006). The potential for Razorbills to come into contact with oil increases significantly during the winter when Razorbills migrate south to the Gulf of St. Lawrence and Gulf of Maine where major shipping routes lie (Wiese and Ryan 2003, Chapdelaine *et al.* 2001).

The management of seabird populations during the non-breeding season has always proven a challenge as the wintering areas and migration routes are seldom well know (Huettmann and Diamond 2000). As a result, a large portion of the monitoring and protection awarded to seabirds is effective only a few months of the year while the birds breed on land (Chapdelaine et al. 2001). Razorbill populations in Atlantic Canada will likely prove an even greater challenge

as we do not fully understand their winter behavior, and on the breeding grounds, populations do not appear to behave independent of one another. It is therefore difficult to detect declining populations and monitor the success of individuals when movement between sites and within colonies is high.

At present levels of hunting mortality and fox predation our model indicates that the Gannet Islands Razorbill population may be in decline while the unaffected MSI population is increasing. There is clearly cause for concern regarding the Gannet Islands population as it is the largest population in North America.

If current conditions persist, the Gannet Islands population may be expected to decline by more than 65% in the next 20 years. Census data indicate that small amounts of Razorbill bycatch may have been sustainable throughout the 1980s and 1990s; however, with deteriorating breeding conditions, previously sustainable levels are no longer sustainable for this population. As a result, we make the following recommendations (1) increase enforcement and education for murre hunters and re-evaluate the timing and quota of the murre hunt with the objective of reducing the hunt in areas where Razorbills are known to aggregate or migrate through, (2) continue the long-term Razorbill demographic monitoring program initiated on the Gannet Islands in 1996 with special emphasis on measuring productivity and determining why nest mortality is high, (3) expand monitoring to other colonies in Labrador that have not been surveyed in many years to determine if these populations are exhibiting similar trends, and (4) immediately begin an annual fox removal program on the Gannet Islands.

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Table 6.1. Summary of the demographic parameters used for the post-breeding population model for Razorbills breeding in Atlantic Canada.

| Parameter | Gannet Islands | Machias Seal Island | Source |
|---|---|---|---|
| Population size (breeding pairs) | 9,808 | 543 | Grecian 2005, Chapdelaine et al. 2001 |
| Pre-breeder survival (age 0-2) | 0.482 | 0.778 | This study |
| Survival (age 3-6) | 0.970 | 0.912 | This study |
| Adult survival (age 7+) | 0.890 | 0.967 | This study |
| Proportion of breeders | | | |
| 1 year old | 0.00 | 0.00 | This study |
| 2 year old | 0.04 | 0.02 | |
| 3 year old | 0.25 | 0.32 | |
| 4 year old | 0.49 | 0.83 | |
| 5 year old | 0.73 | 0.94 | |
| 6 year old + | 1.00 | 1.00 | |
| Fecundity | 0.39 | 0.56 | This study |

| | | | |
|---|---|---|---|
| Hunting mortality[a] | 500-3000 | 0 | Elliot 1991, Chapdelaine 1997 |

[a]Total number of Razorbills shot from all colonies in Newfoundland, Labrador, and Quebec.

Table 6.2. Records of Arctic foxes on the Gannet Islands, 1978-2006 (data up to 1999 from Robertson and Elliot 2002).

| Year | Comments |
|---|---|
| 1978 | No evidence of recent or current fox presence |
| 1981-83 | No evidence of recent or current fox presence |
| 1992 | 4 adult foxes and 2 pups on GC2 and GC5. Found evidence that foxes have been on the islands for several years prior to 1992. |
| 1993 | No evidence of recent or current fox presence |
| 1995 | 1 adult fox on GC2 (only GC2 and GC4 checked). Evidence of a fox on GC4. All Razorbill colonies on both islands abandoned, many dead adult Razorbills. |
| 1996 | 1 adult fox on GC2, moved to GC1 in June (stayed for entire summer) |
| 1997 | 1 adult fox on GC3 in late June, evidence of fox on GC4 |
| 1998 | 1 adult fox on GC5 in July |
| 1999 | No evidence of recent or current fox presence (polar bear present) |
| 2000 | 1 adult fox on GC5. Only 8 chicks on island. |
| 2001 | 1 adult fox on GC5. Laying not initiated. |
| 2002 | 1 adult fox on GC2 |
| 2003 | No evidence of recent or current fox presence |
| 2004 | No evidence of recent or current fox presence |
| 2005 | Large adult fox seen on GC5 on approx. Aug 10, very few birds present |
| 2006 | No evidence of recent or current fox presence |

Table 6.3. Number of occupied breeding sites in permanent Razorbill study plots on the Gannet Islands, Labrador, 1978-2006 (data up to 1999 from Robertson and Elliot 2002).

| Plot | 1978 | 1983 | 1984 | 1992[a] | 1998 | 1999 | 2003 | 2004 | 2005 | 2006 | % change 1983-84 to 2003-06 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| GC1-a | - | 120 | 134 | - | 153 | 124 | - | - | - | - | - |
| GC1-b | - | 110 | 113 | 121 | 165 | 126 | - | - | - | - | - |
| GC2-a | 125 | 118 | 123 | 0 | 37 | 55 | 36 | 33 | 28 | 39 | -72 |
| GC2-b | 23 | 32 | 30 | 0 | 13 | 21 | 15 | 18 | 13 | 19 | -48 |
| GC2-c | 92 | 93 | 108 | 0 | 55 | 70 | 57 | 50 | 65 | 59 | -53 |
| GC2-d | - | 46 | 50 | 0 | 23 | 25 | 81 | 78 | 73 | 87 | +39 |
| GC2-e | - | 52 | 53 | 0 | 26 | 37 | 43 | 45 | 46 | 61 | -8 |
| GC3-a | - | 56 | 43 | 22 | 55 | 44 | - | 102 | - | 110 | +54 |
| GC4-a | - | 45 | 32 | 7 | 36 | 46 | - | - | - | - | - |
| GC5-a | - | - | 27 | 0 | 21 | 54 | 75 | - | - | 81 | - |
| GC5-b | - | - | - | - | - | 109 | 129 | - | - | 119 | - |

[a]Foxes present on GC2 and GC5, evidence of foxes on GC4

Figure 6.1. Seasonal distribution of recoveries of banded Razorbills (n = 21) from the Gannet Islands, Labrador shot during the murre hunt, 1996-2005.

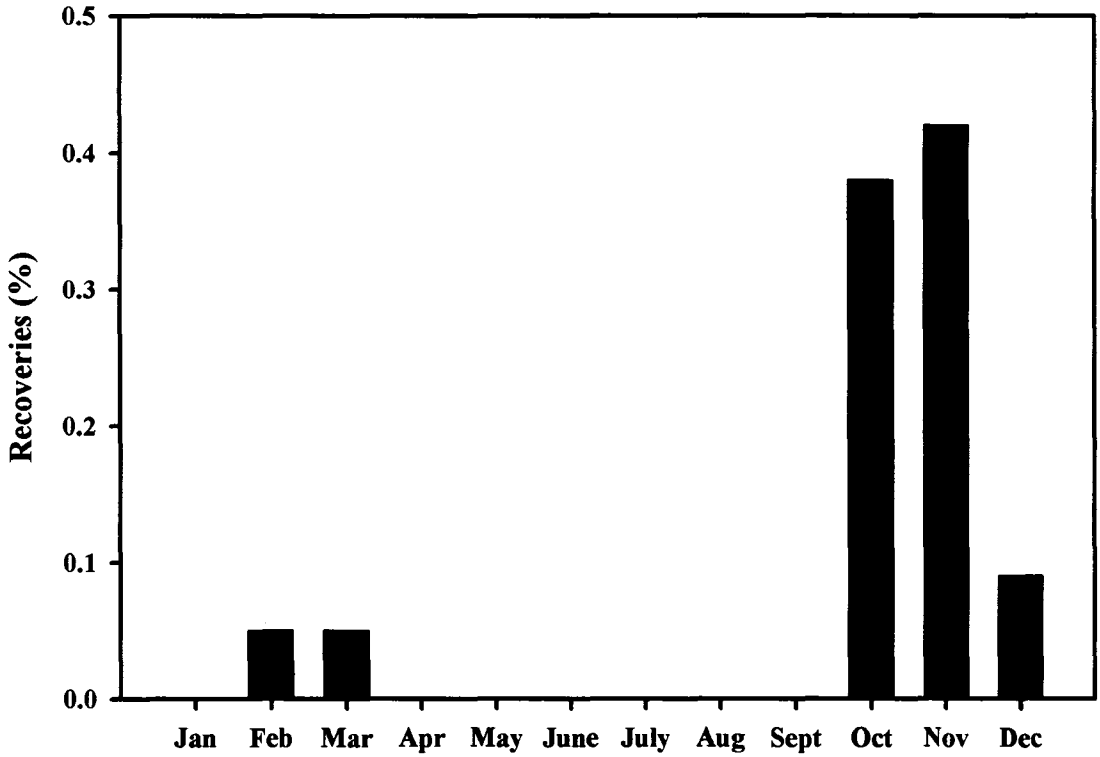


Figure 6.2. Location of recoveries of Razorbills (n = 20) banded on the Gannet Islands during 1996-2005.

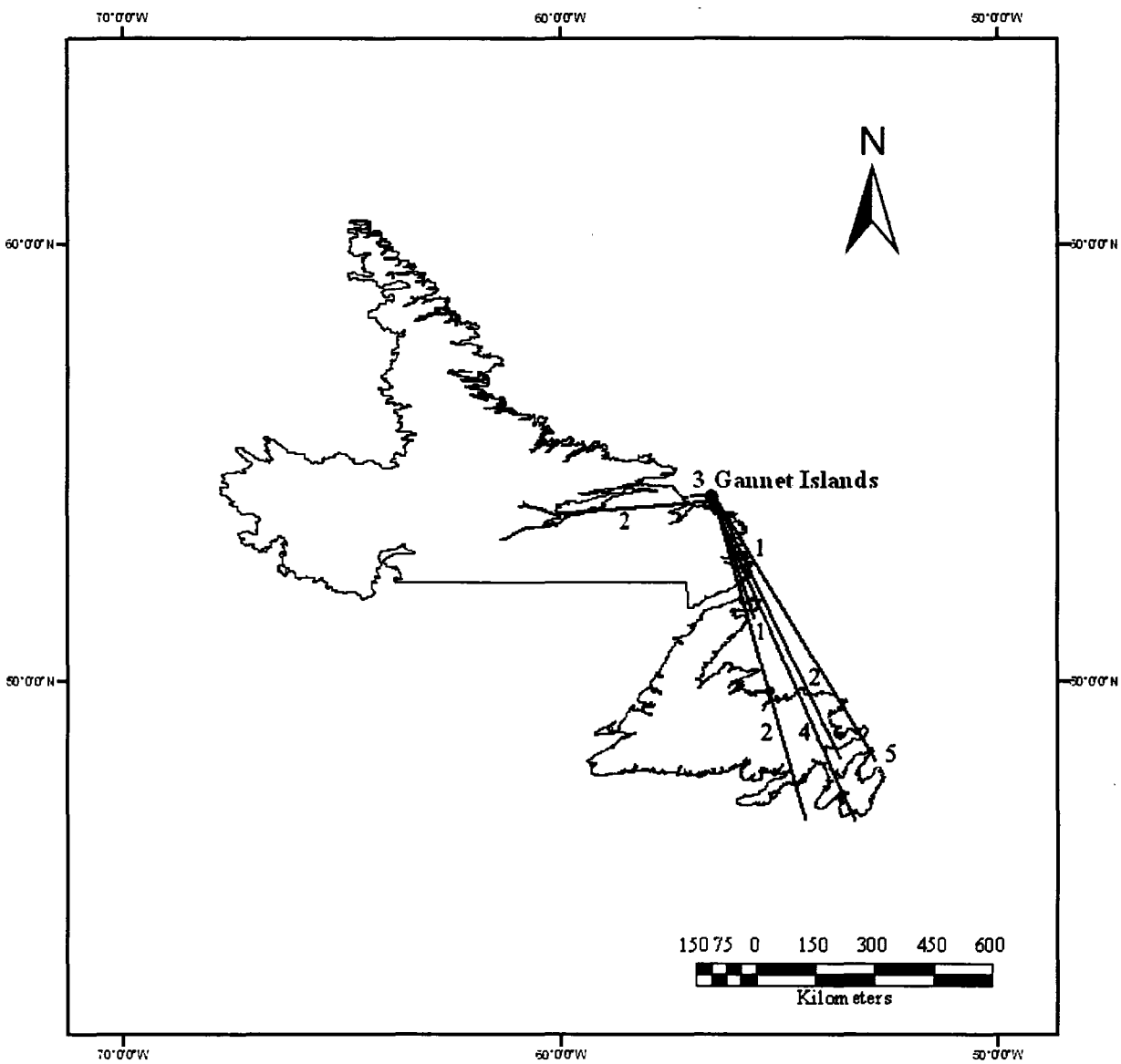


Table 6.4. Recoveries of Razorbills shot in the murre hunt with respect to age, 1925-2005.

| | 0-1 yr | | 2-4 yr | | 5+ yr | | |
|---|---|---|---|---|---|---|---|
| Years | N | % | N | % | N | % | Source |
| 1925-1994 | 52 | 60 | 30 | 34 | 5 | 6 | Chapdelaine 1997 |
| 1996-2005 | 22 | 96 | 1 | 4 | 0 | 0 | This study |

Table 6.5. Deterministic growth rates for eight models projected over 20 years. Subscripts reflect different factors in the model (MSI = Machias Seal Island, Hunt = hunting bycatch, Fox = fox predation, $S_p$ = pre-breeder survival (age 0-2), $S_{3\text{-}6}$ = annual survival for birds age 3-6 years, $S_a$ = adult survival (age 7+ years), $F_a$ = fecundity, $\lambda$ = intrinsic rate of increase, t = time in years). Effect is calculated as the difference in growth rate relative to the Gannet Islands baseline growth rate which incorporates MSI $S_p$.

| Site | Scenario | Hunt[a] | Fox | $S_p$ | $S_{3\text{-}6}$ | $S_a$ | $F_a$ | $\lambda$ | Effect | N (t=1) | N (t=20) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Gannet Islands | Current conditions | 0 | 0 | 0.482 | 0.970 | 0.890 | 0.195 | 0.9475 | -0.0603 | 17,000 | 5,784 |
| | Baseline | 0 | 0 | 0.778 | 0.970 | 0.890 | 0.195 | 1.0078 | - | 17,000 | 19,854 |
| | Fox predation | 0 | Y | 0.778 | 0.970 | 0.890 | 0.195 | 0.9952 | -0.0126 | 17,000 | 15,435 |
| | Hunting mortality | 700 | Y | 0.778 | 0.970 | 0.890 | 0.195 | 0.9458 | -0.0620 | 17,000 | 5,576 |
| | 5% hunt mortality | 1,297 | Y | 0.778 | 0.970 | 0.890 | 0.305 | 0.9211 | -0.0867 | 17,000 | Extinct[b] |
| | Increased $F_a$[c] | 700 | Y | 0.778 | 0.970 | 0.890 | 0.305 | 1.0239 | +0.0161 | 17,000 | 30,085 |
| Machias Seal Island | Current conditions | 0 | 0 | 0.778 | 0.912 | 0.967 | 0.294 | 1.0613 | - | 1,080 | 3,120 |

[a]Annual bycatch (n), females only (96% first year birds, 4% second year birds).

[b] Time to extinction (N(t)) = 10 years, Elliot 1991

[c] Sources: Birkhead and Nettleship 1983, Hipfner and Bryant 1997

Figure 6.3. Gannet Islands (a) and Machias Seal Island (b) stable age distribution.

$$w = \begin{pmatrix} 0.2107 \\ 0.1069 \\ 0.0543 \\ 0.0555 \\ 0.0567 \\ 0.0579 \\ 0.0591 \\ 0.3989 \end{pmatrix} \quad \begin{matrix} (a) \\ \\ \\ \\ \\ \\ \\ \\ \end{matrix} \qquad \begin{pmatrix} 0.1873 \\ 0.1310 \\ 0.0547 \\ 0.0557 \\ 0.0557 \\ 0.0578 \\ 0.0589 \\ 0.3989 \end{pmatrix} \quad \begin{matrix} (b) \\ \\ \\ \\ \\ \\ \\ \\ \end{matrix}$$

Figure 6.4. Gannet Islands (a) and Machias Seal Island (b) elasticity matrices.

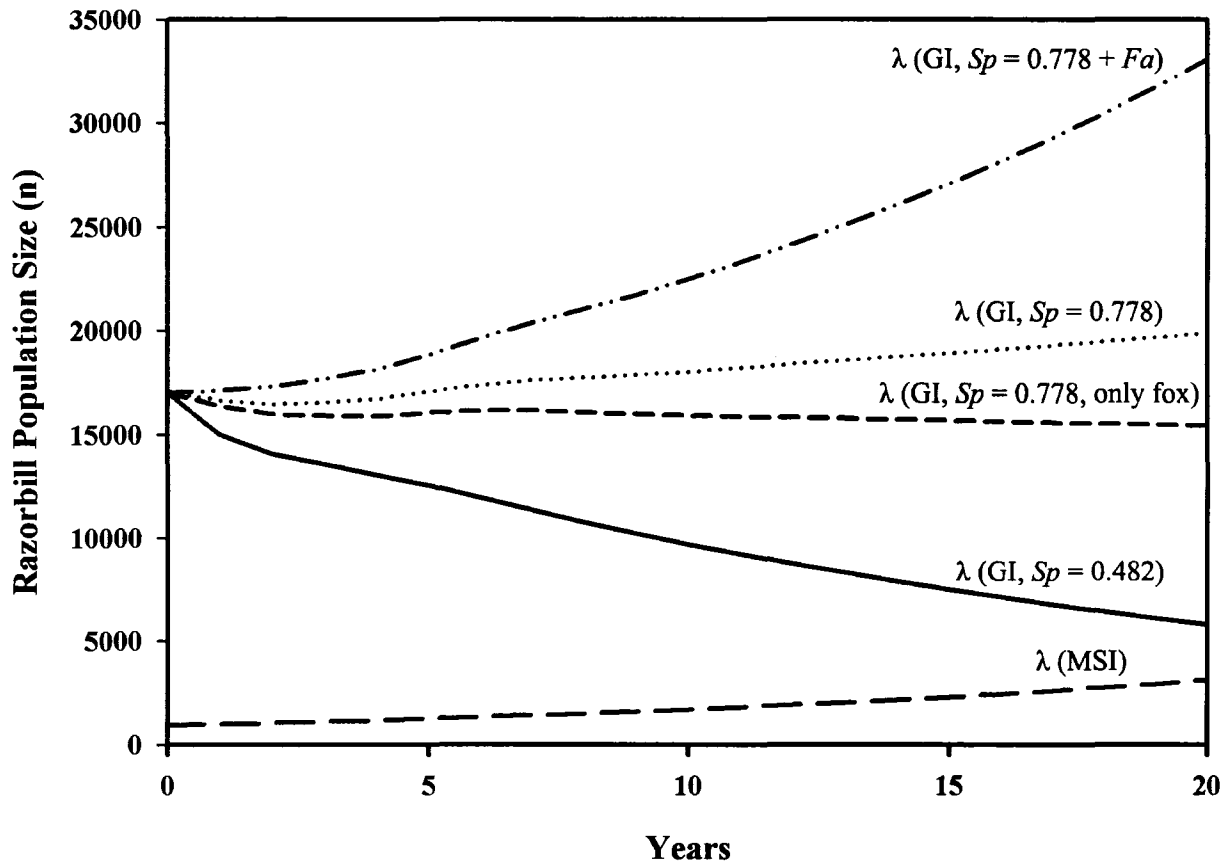
(a)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 0 | 0 | 0 | 0 | 0.0027 | 0.0027 | 0.0028 | 0.0414 |
| 0.0496 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.0496 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0.0496 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0.0496 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0.0469 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.0442 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0.0414 | 0.6195 |

(b)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 0 | 0 | 0 | 0 | 0.0063 | 0.0054 | 0.0047 | 0.0489 |
| 0.0652 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.0652 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0.0652 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0.0652 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0.0590 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.0535 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0.0489 | 0.5124 |

Figure 6.5. Deterministic, density independent growth curves during a 20 year projection for Razorbills breeding on the Gannet Islands affected by both fox predation and hunting bycatch [λ (GI, $S_p$ = 0.482)], in the absence of both fox predation and harvest [λ (GI, $S_p$ = 0.778)], for the same population only affected by fox predation [λ (GI, $S_p$ = 0.778, only fox)], and both fox predation and hunting, but with 1980s Gannet Islands fecundity ($F_a$ ) values taken from Birkhead and Nettleship (1983) [λ (GI, $S_p$ = 0.778 + $F_a$)]. The baseline projection for MSI is also shown [λ (MSI)].



# CHAPTER SEVEN

# SUMMARY

Seabird colony dynamics can be influenced by biological factors such as food availability and predators (Chapters 3 and 5; Hobson et al. 1999, Oro et al. 2003) and by factors associated with human activity (Chapters 4 and 6; Tasker and Becker 1992, Martínez-Abraín et al. 2002). This dissertation has undertaken the study of both types of factors and their influence on an uncommon and vulnerable seabird, the Razorbill (*Alca torda*). The works carried out (eight manuscripts, five of which are presented in this dissertation) have utilized a variety of scientific methods to address specific questions relating to Razorbill demography and population dynamics whose answer was necessary for the protection of the species. This is therefore a thesis of applied science and, more importantly, a thesis on the biology of conservation.

## 1.1. DEMOGRAPHIC PARAMETERS

In order to demonstrate the significance of the parameter estimates reported in this dissertation, I review what has been previously reported for Razorbills.

### *1.1.1. Survival*

I am aware of only one previous estimate of adult and pre-breeder survival for Razorbills in North America. Chapdelaine (1997) estimated survival in Razorbills breeding in the Gulf St. Lawrence during 1986-1995, and although the results are valuable, the methods used to estimate pre-breeder survival were imprecise and did not account for natural variation in the level of mortality between fledging (when mortality is typically the highest) and age four. Elsewhere in

the species range, estimates of adult survival are relatively abundant (Lloyd 1974, Lloyd and Perrins 1977, Steventon 1979, Harris and Wanless 1989); however I am aware of only one study that estimated pre-breeder survival for the species. Lloyd and Perrins (1977) estimated survival from fledging to age four using return rates for Razorbills on Skokholm Island and Skomer, United Kingdom.

To my knowledge, only one other study on the relationship between Razorbill survival and climate exists (Sandvik et al. 2004). In contrast to my study that found that local climate covariates such as ocean temperature were most strongly correlated with survival, Sandvik et al. (2004) found that the North Atlantic Oscillation, a large-scale index of ocean pressure (not temperature), was the most strongly correlated with Razorbill survival in Norway.

### *1.1.2. Dispersal*

This study is the first to address philopatry, breeding dispersal, and long-distance movements of Razorbills breeding in the Northwest Atlantic region. A small number of studies on philopatry exist for Europe, but breeding dispersal has not been reported and all records of long-distance movement were from recoveries of birds shot during migration (i.e. outside the breeding season; Lloyd 1974, Mead 1974, Lloyd and Perrins 1977, Harris and Wanless 1989, Bakken et al. 2003, Lyngs 2003) and do not fall within the scope of this dissertation.

### *1.1.3. Productivity, diet, and kleptoparasitism*

Razorbill productivity rates have been quantified in numerous studies throughout North America and Europe (Lloyd 1979, Chapdelaine and Laporte 1982, Birkhead and Nettleship 1983, Barrett

1984, Lyngs 1994, Chapdelaine and Brousseau 1996, Hipfner and Bryant 1999). However, the productivity rates recorded on the Gannet Islands during 2004-2006 are the lowest in North America and are comparable to only one study in Europe involving a highly disturbed plot on Graesholmen, Denmark during 1985-1986 (Lyngs 1994).

This study is the first to report on intraspecific kleptoparasitism in Razorbills. The rates of intraspecific kleptoparasitism reported for Razorbills on the Gannet Islands are the highest reported for any seabird. Poor productivity on the Gannet Islands during the same time period (2003-2006) as this behavior was observed is in part thought to be due to an inability of adult birds to provision their chicks due to theft. This behavior was not observed at any other Razorbill colony in North American during the same time period, suggesting that feeding conditions on the Gannet Islands differ from other colonies where birds do not appear to have difficulty finding food.

## 2.1. IMPLICATIONS FOR RAZORBILLS AND OTHER LONG-LIVED SEABIRDS

### *2.1.1. Razorbill demography*

Seabirds have life-history traits, already described in this dissertation, which determine precise selective values of the different components of seabird populations. Local recruitment in seabirds is relatively low, since productivity is low and they show delayed sexual maturity, whereas adult mortality is low due to the low number of predators and a conservative reproductive strategy (Weimerskirch 2002). Thus, local population growth of seabirds is very sensitive to changes in adult survival (i.e. has the highest elasticity) such that a 3% decrease in survival can have a greater impact than a decrease of 30% in breeding success or other

demographic parameters such as juvenile survival (Weimerskirch 2002). At the Gannet Islands, Razorbill adult and pre-breeder survival and productivity are all low; therefore it is not surprising that the population is predicted to decline. These results allow two basic types of conclusions for management. First, if the survival values, especially adult survival, can be increased, this will result in a much greater enhancement of the population growth rate ($\lambda$) than would a similar increase in reproduction (Morris and Doak 2002). Second, the predictions of current population growth in the case of MSI or decline at the Gannet Islands, hinge critically on the estimate of adult survival. If this estimate is even somewhat inaccurate, growth could be much higher or lower than expected.

In this study, we attempted to account for bias in the survival estimate as a result of band resighting errors through establishing strict protocols to assist in the detection of errors. We also attempted to account for bias that results from the dispersal of birds that moved outside the sampling area through the inclusion of resightings from the Gulf of Maine and Herring Islands. Accurate estimation of the demographic parameters is the first step of any conservation based program, and given that the Gannet Islands Razorbill population is expected to decline, the next step is to determine what can and needs to be done to reverse this trend. At the Gannet Islands, adult survival is somewhat low, but within the acceptable range for the species, therefore it may be better to manage for increased survival of juveniles or productivity (Morris and Doak 2002). With the cooperation of hunters and government, it may be possible to reduce hunting bycatch and raise pre-breeder survival to a level comparable to what is seen on MSI. Also, past studies of Razorbill productivity at the Gannet Islands have reported much higher rates (0.46 to 0.73) than are currently observed, suggesting that higher productivity rates are biologically feasible for

Razorbills (Birkhead and Nettleship 1983, Hipfner and Bryant 1999). Determining what factors are currently causing low productivity (fox predation has been established as a contributing factor in this dissertation; see Chapter 6), and there is some evidence that kleptoparasitism and lack of food play a strong role, see Chapter 5) would be highly beneficial for the population.

*2.1.2. The importance of dispersal in population dynamics*

Dispersal is a central theme that has generated a lot of theoretical studies on life-history, population regulation, density-dependence, and conservation management (Greenwood and Harvey 1982, Clobert and Lebreton 1991). Until recently, detailed, quantitative studies on dispersal in seabirds were rare, likely due to an abundance of single-site studies and the challenges of tracking large numbers of birds over great distances (Coulson 1991, Wooller et al. 1992, Lindberg et al. 1998, Cam et al. 2004).

For many years it was believed that most colonial seabirds exhibited high levels of philopatry and breeding site fidelity (Boyd 2001). However, recent studies have identified dispersal as a key parameter affecting local population dynamics of long-lived seabirds (Frederiksen and Petersen 2000, Breton et al. 2006a). Traditionally, the most widely considered consequence of dispersal to local populations has been population regulation through density-dependent emigration (Hanski 2001). However, dispersal has also been shown to affect the size and dynamics of local populations in other ways including the maintenance of populations which would otherwise be declining and establishment of new populations (Hanski 2001).

The results of this study suggest that processes occurring among local Razorbill populations (i.e. disturbance, predation, and weather) may be responsible for modifying numbers at each population, both on a local and regional scale. In the case of the Gannet Islands, population counts suggest that this population is increasing; however estimates of the demographic parameters and results of the population trajectory do not support this trend. Dispersal and recruitment of birds from other populations is implicated in the maintenance of this population and the recolonization of the Gulf of Maine islands.

*2.1.3. Cumulative mortality studies*

All birds are exposed to a variety of adversities that potentially decrease their survival or reproductive success. These include weather, food shortages, predators, competitors, parasites, disease, and human-induced effects (Burger and Gochfield 1990, Weimerskirch 2002). Each factor affects seabirds in a different way, but more importantly, factors can also interact and create impacts far greater than any one factor alone (Burger and Gochfield 1990). For example, Wiese et al. (2004) found that the cumulative impact of mortality from hunting and oiling is reducing the ability of Thick-billed Murre (*Uria lomvia*) populations to grow and Wendt and Cooch (1984) warned that the kill of murres, if added to the impact of decreasing prey stocks, gill nets, and oiling mortality, leaves little room for populations to buffer against increased mortality in especially poor years. In the Marbled Murrelet (*Brachyramphus marmoratus marmoratus*), population declines in Alaska are thought to be due to the cumulative effects of oil pollution, gill netting, and logging of old-growth breeding habitat (Piatt and Naslund 1995). In Razorbills, the effect of fox predation reduced the Gannet Islands population growth rate by 1.26%, which at first may not seem significant. However, the cumulative effects of fox

predation and hunting mortality at the Gannet Islands appear to be reducing the population growth rate by more than 7% and if correct are clearly not sustainable. This study emphasizes the need to consider multiple sources of mortality when developing management plans for the conservation of vulnerable species. If important factors are not identified or are ignored, effort may be concentrated on parameters or sources of mortality which are not the most crucial for the population, resulting in ineffective management.

*2.1.4. The suitability of parameter estimates from other populations*

Concurrent, long-term, multi-site demographic studies are rare; therefore this project provided an ideal situation to address whether parameters from one population can be substituted for another when they are not already available. In many seabird studies, parameter estimates from the population of interest are not available and researchers rely on published results for other nearby populations or in some cases, closely related species (see Murphy et al. 1999, Lewison and Crowder 2002, Wiese et al. 2004). In some cases it is not possible to estimate certain parameters, either because sample sizes are too low or the population is declining at a rapid rate and the long-term capture-mark-recapture (CMR) programs necessary to estimate survival are not feasible (Green and Hirons 1991). This is often the case with critically endangered species. However, in most seabirds, adult survival rates are not constant and may vary among populations depending on environmental factors influencing individuals. For Razorbills, environmental conditions are correlated with annual variation in survival within and between colonies (see Chapter 4) and differences in diet and feeding behavior between colonies may explain contrasting trends in productivity (see Chapter 5). Similar trends have also been reported in Cassin's Auklets breeding in the north Pacific where local populations show different adult

survival probabilities, likely due to environmental conditions (Gaston 1992, Bertram et al. 2000, Bertram et al. 2005). Therefore, it appears that even within members of the same species, the demographic parameters from one population cannot be easily substituted for another.

### *2.1.5. Final conclusions*

The recurring conclusion from this study and highlighted by the population trajectory analysis in Chapter 6 is that continued monitoring and reassessment of Razorbill population parameters, especially dispersal, survival, and productivity, are required as mitigation plans are developed and implemented. The viability of the Razorbill population at their largest Canadian colony, the Gannet Islands, is in doubt. Future research should focus on obtaining better estimates of adult and pre-breeder survival through the banding of large numbers of individuals and estimation of band resighting error and ways to account for this error in CMR studies. Given the significance of inter-colony and year variability in survival and productivity, continued collaboration between researchers on the Gannet Islands and MSI would prove highly beneficial. Future studies should give strong consideration to the role of dispersal, unless it can be shown that dispersal does not occur in the focal species, then the accuracy of survival probabilities will be compromised when studies are confined to a single local population. In view of the situation at the Gannet Islands, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) needs to revisit the case of the Razorbill and consider listing it as a species of special concern. The Newfoundland murre hunt needs further study and enforcement to reduce the damaging kills of Razorbills that appear to be occurring. And finally, I hope that this dissertation has demonstrated that cooperative research among researchers and organizations is an efficient and productive way to

expand the spatial coverage of a study and obtain reliable estimates of dispersal, survival, and other demographic parameters.

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